NON-NATIVE PLANT INVASION OF BOREAL FOREST GAPS: IMPLICATIONS FOR STAND REGENERATION IN A PROTECTED AREA SHAPED BY HYPERABUNDANT HERBIVORES

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Non-native plant invasion of boreal forest gaps:

Implications for stand regeneration in a protected area shaped by hyperabundant herbivores

by

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ABSTRACT

While Canada thistle (*Cirsium arvense*) is notorious as an aggressive, invasive non-native weed in agricultural fields, grasslands, and roadsides throughout North America, it has not typically posed a threat to boreal forests. However, in the balsam fir (*Abies balsamea*) -dominated lowland boreal forests in Gros Morne National Park (GMNP- Newfoundland, Canada), Canada thistle has recently invaded natural areas on a large landscape scale, occurring in 42% to 55% of anthropogenic and natural forest gaps, respectively, and frequently forming dense monocultures. It is important to determine if and how Canada thistle invasion will affect regeneration of native trees, particularly since regeneration of gaps in GMNP is already threatened by non-native, hyperabundant moose (*Alces alces*) populations, which exert extreme browsing pressure on forests. This study assessed the condition of forest gaps to support conifer regeneration by describing the current level of balsam fir regeneration, quality of seedbeds, and degree of Canada thistle invasion. Balsam fir seed and seedling addition experiments were performed in gaps to determine the effect of thistle presence on emergence, growth, and survival of balsam fir. Finally, the potential for allelopathic impacts on native conifers from Canada thistle was assessed in greenhouse experiments. Results revealed that gaps are not regenerating, contain poor seedbeds for conifer recruitment, and are heavily disturbed by moose browsing. Canada thistle invasion further threatens balsam fir emergence and early seedling survival. However, older, transplanted fir seedlings were not negatively affected by thistle, suggesting that seedling planting may be an effective management strategy to

encourage fir regeneration in thistle-invaded gaps, and potentially even phase out shade-intolerant thistle plants over time.

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1. INTRODUCTION AND OVERVIEW

Description of the problem

In boreal ecosystems, disturbance is a fundamental process that ensures the persistence of forest structure and function (Shugart et al. 1992, Elliot-Fisk 2000). Natural disturbances such as insect outbreaks, windfalls, and fire ensure patchiness and diversity in the boreal forest landscape and encourage forest renewal (Shugart et al. 1992). In the balsam fir (*Abies balsamea* (L.) Mill.) -dominated boreal forests of northeastern North America, balsam fir is well adapted to regenerate after cycles of natural (i.e. insect outbreaks) and anthropogenic (i.e. harvesting) disturbances since these processes usually preserve and favour the growth of its pre-established seedling bank (i.e. advanced regeneration) (Hatcher 1960, Hall and Richardson 1973, Osawa 1994, Duchesneau and Morin 1999, Noel 2004).

However, in the balsam fir forests of Gros Morne National Park (GMNP), these cycles of disturbance and regeneration have been dramatically altered. As a result of sustained browsing pressure by hyper-abundant populations of non-native moose (*Alces alces* L.), disturbed forest gaps formed up to 30 years ago (i.e. since the late 1970's) are experiencing regeneration failure and have not returned to the expected closed canopy, balsam fir-dominated forest (McLaren et al. 2000, McLaren et al. 2004, Burzynski et al. 2005, Forbes 2006). Even before the onset of a gap-generating disturbance, moose heavily browse the advanced regeneration of balsam fir (Rose 2002), threatening the ability of this species to regenerate after disturbance since it does not form a seed bank (Frank and Safford 1970, Morin and Laprise 1997, Duchesneau and Morin 1999, Greene

et al. 1999, Parent et al. 2003). When disturbances occur, moose concentrate their browsing activities in these early successional assemblages since they are re-vegetated with highly palatable species (Rose and Hermanutz 2004, Forbes 2006, Gosse 2006). This maintains conditions of disturbance and results in heavy trampling of native seedbeds (Rose and Hermanutz 2004). Consequently, rather than regenerating to closed-canopy boreal forests, many disturbed sites remain as open landscapes with reduced native tree species diversity and severely compromised forest structure and ecological integrity (McLaren et al. 2004, Burzynski et al. 2005, Forbes 2006).

Recent studies have noted the occurrence of invasive alien plants in forest gaps in GMNP. Rose and Hermanutz (2004) found non-native plants such as creeping buttercup (*Ranunculus repens* L.), coltsfoot (*Tussilago farfara* L.), common dandelions (*Taraxacum officinale* Weber), and hawkweeds (*Hieracium* spp.) in gaps disturbed by timber harvesting and insect infestations. Hendrickson et al. (2005) documented the invasion of non-native coltsfoot throughout forest disturbances in GMNP, and noted that invasion has been greatly facilitated by management activities involving the importation of bedrock aggregate that neutralizes or buries unfavourable acidic soils and transports rhizome fragments derived from plants established in aggregate stockpiles. Alien plant invasions can present severe threats to native species diversity, ecological integrity, ecosystem structure and function, and human welfare (Vitousek et al. 1997, Kolar and Lodge 2001, Levine et al. 2003). Disturbance is a key factor enabling biological invasions because it causes a sudden flush of surplus resources such as light, nutrients, or water, removes or limits competition, and creates microsites on bare ground (Brothers

and Spingarn 1992, Cronk and Fuller 1995, Burke and Grime 1996, Stohlgren et al. 1999). Yet alien plant invasion is not normally a major problem in the boreal regions as forests act as a relatively continuous barrier to wind dispersal of alien plant seeds (Brothers and Spingarn 1992) and the low light and nutrient availability and low soil pH in dense evergreen forest canopies, which often separate gap openings by great distances, provide sub-optimal growing conditions for resource-demanding alien plants (Bakker 1960, Shugart et al. 1992, Haber 1997, Elliot-Fisk 2000, Rose 2002). Despite the fact that Canada's National Parks often contain hundreds of introduced plants (Mosquin 1997), the vast majority of non-native plants occur in highly anthropogenically- disturbed areas such as roadsides, picnic areas, campgrounds, ditches, gravel pits, hiking trails, and other areas frequented by people (Mosquin 1997, Rose 2002). However, in GMNP, moose are not only generating ideal conditions for alien plant establishment in gaps by maintaining conditions of disturbance including high light availability and bare ground (Burke and Grime 1996, Stohlgren et al. 1999, Rose and Hermanutz 2004), but also appear to be conduits for the transport of alien plant propagules into remote forest sites.

The greatest threat to ecosystem functioning and native species diversity is posed when an alien species successfully expands its range into natural or recovering protected ecosystems that are remote from human activity (Burke and Grime 1996, Mosquin 1997, Hendrickson 1999, Rose and Hermanutz 2004). In GMNP, Canada thistle (*Cirsium arvense* (L.) Scop.), an alien herb in North America, has recently invaded protected boreal forest gaps created through either natural or anthropogenic disturbance (Figure

a)

b)

Figure 1.1 – Photographs taken in Gros Morne National Park in the summer of 2006 of dense, invasive Canada thistle monocultures in *a)* a non-regenerating natural gap disturbed by an insect outbreak in 1977, and *b)* a non-regenerating anthropogenic gap disturbed by domestic harvesting in 1997.

1.1). This invasion is already on a large scale; surveys throughout the Park in 2005 indicated its presence in 55% of gaps disturbed by outbreaks of eastern spruce budworm (*Choristoneura fumiferana* Clem.) and hemlock looper (*Lambdina fiscellaria fiscellaria* Guenee), and in 41% of gaps created by legal small-scale, traditional domestic harvesting by local residents (Parks Canada, unpublished data). Many of these invaded gaps are in remote locations and are surrounded by relatively continuous boreal forest canopy. The degree of invasion by Canada thistle was unanticipated as it has not generally been considered a threat to boreal forests (Haber 1997). Rather, it is best known as a noxious weed primarily within natural grassland and agricultural ecosystems (Moore 1975, Donald 1990), roadsides, waste places, ditches, and abandoned fields (FNA 2007).

Study species: Canada thistle

Canada thistle (also referred to as creeping thistle, Californian thistle, or field thistle) is an erect herbaceous perennial in the Asteraceae family that generally ranges in height from 30-150 cm and is distinguished from all other thistles by its: 1) creeping horizontal roots containing adventitious buds; 2) dense clonal growth; and 3) small (<2.5 cm) dioecious capitula (Nuzzo 1997). Canada thistle is a long-day plant (Hunter and Smith 1972) and in Newfoundland, flowering normally begins in July and may continue into September. Seeds are achenes with an attached pappus of numerous plumose bristles (Nuzzo 1997). Shoots in any clonal patch are either all male or all female, and although seed production primarily occurs in female plants, up to 26% of "male" plants are self-fertile hermaphrodites or sub-hermaphrodites that occasionally produce small quantities

of seed (Kay 1985, Fenner and Thompson 2005). It thrives in both dry (e.g. sand dunes; sandy fields) and wet (e.g. stream banks; lakeshores; cleared swamps; muskeg; ditches) habitats (Moore 1975, Nuzzo 1997, Zouhar 2001), tolerating annual precipitation ranging from 305-1015 mm per year and growing best with 400-750 mm of precipitation per year (Zouhar 2001). Throughout its range, Canada thistle prefers deep, well-aerated, mesic soils and frequently grows in a large variety of substrates including clay, clay loam, silt loam, sandy loam, sandy clay, sand dunes, gravel, limestone, and chalk, but not peat (ISSG 2007).

Canada thistle is native to southeastern Europe and the eastern Mediterranean and has long been a pervasive non-native weed in agricultural and other chronically disturbed landscapes throughout North America and in temperate zones throughout the world, including South America, Australia, New Zealand, southern Africa, and the United Kingdom (Moore 1975, Kazinczi et al. 2004). It was first accidentally introduced to North America in the early 1600s (Nuzzo 1997), likely as a contaminant of crop seed (ISSG 2007). It was most likely introduced on more than one occasion, particularly within French settlements in Canada (Hansen 1918). After initial introduction, Canada thistle spread rapidly throughout North America, becoming common in Montreal by 1821 (Rousseau 1968), for example, and new unintentional introductions resulting from both natural transboundary dispersal as well as agricultural activities furthered its spread (Nuzzo 1997, ISSG 2007). Seeds were most likely dispersed through translocation of crop seeds, hay, and farm machinery and may have also been spread in livestock feces as well as irrigation water (Nuzzo 1997). By 1991, Canada thistle had been declared a

noxious weed (an invasive plant specified by provincial, state, and/or federal legislation as being particularly troublesome and warranting control) by at least 35 U.S. states and six Canadian provinces (Moore 1975, FNA 2007). It is currently established as an invasive weed in all Canadian provinces and territories and in 44 U.S. states (FNA 2007, ISSG 2007). Its initial date of introduction into Newfoundland is unknown, but given the province's long history of European settlement, it is likely that Canada thistle was introduced during, or prior to, the 1700's (John E. Maunder, personal communication, 2007).

Why Canada thistle invasion warrants concern by Park managers

Despite its lack of invasion history in boreal forests, Canada thistle has efficiently infiltrated protected forests in GMNP and has invaded widely scattered, remote boreal forest gaps over an extensive landscape scale. Many of these gaps are surrounded on all sides by dense evergreen canopy and are often located many kilometers from the nearest road. The extent of Canada thistle's distribution should be viewed as a serious threat to ecological integrity within GMNP for a variety of reasons, outlined below.

History of invasion and ecological impacts

Throughout its range, Canada thistle has demonstrated a tendency to become highly invasive and decrease native plant and animal species diversity (Stachon and Zimdahl 1980, Mosquin 1997), alter natural ecosystem structure and composition (Nuzzo 1997, Zouhar 2001), and contribute to the elimination of endangered and/or endemic

plant species (Cheater 1992). In North America, natural communities such as prairies, barrens, savannas, glades, sand dunes, and meadows that have undergone disturbance and/or are undergoing ecosystem restoration are particularly threatened by Canada thistle (Hutchison 1992, White et al. 1993). For example, Stachon and Zimdahl (1980) reported that species diversity in Colorado grassland was inversely proportional to the relative frequency of Canada thistle. In agroecosystems, the species severely reduces crop yields and limits livestock grazing due to the physical hazards posed by its sharp spines, resulting in millions of dollars in economic damage in southern Canada and the continental U.S. (Moore 1975, Donald 1990, Skinner et al. 2000).

High capacity for growth, reproduction, and spread

Canada thistle is a pervasive invader of native plant communities due to its high capacity for vegetative and sexual reproduction, which enables rapid growth and range expansion (Moore 1975, Nadeau and Vanden Born 1989, Donald 1994, Heimann and Cussans 1996). Levine (2000) notes that unlike many invasive, non-native plant species, Canada thistle invasion is not influenced by local native species diversity. Germination normally occurs in the spring, but rosettes may be formed in late summer immediately after seed dispersal (Heimann and Cussans 1996). Beginning a few weeks after germination, a Canada thistle seedling undergoes rapid clonal growth and forms a perennial, creeping horizontal root system that contains numerous adventitious buds from which new shoots are readily recruited (Hamdoun 1972, Donald 1994, Dock Gustavsson 1997). A single plant can potentially produce 26 adventitious shoots, 154 adventitious

root buds, and 111 m of roots after 18 weeks of growth (Nadeau and Vanden Born 1989). Well established clones can spread up to 12 m per year (Chancellor 1970) and as a result, just one established Canada thistle plant can lead to a large infestation (Moore 1975).

Canada thistle also undergoes range expansion through production of large quantities of light, plumed seeds that are easily transported by both wind and water (Trumble and Kok 1982, Heimann and Cussans 1996, Nuzzo 1997). Efficient long-distance wind dispersal in this species is attributed to a high pappus diameter to achene diameter ratio and subsequent low terminal velocities of seeds (Sheldon and Burrows 1973, Fenner and Thompson 2005). Although up to 30,000 viable seeds/m^2 may be produced within dense thistle patches each year, few seeds are formed unless male and female plants are within 50-90 m of each other (Bakker 1960, Amor and Harris 1974). Seeds can remain viable for up to 21 years in soil (Goss 1924, Toole and Brown 1946) and can form a persistent seed bank to facilitate invasion when appropriate conditions of disturbance arise (Eber and Brandl 2003). Seed germination is usually initiated by exposure of alternating high temperatures (25-30 °C), but at lower temperatures, germination is aided by high light intensities (Bakker 1960, Amor and Harris 1974, Heimann and Cussans 1996).

Strong competitive abilities

As a result of its rapid growth rates and extensive spreading root network, Canada thistle is a strong competitor for resources such as water, nutrients, light, and space and thus is able to 'crowd out' and displace neighbouring vegetation within ruderal

communities (Donald 1990, Zouhar 2001, Eber and Brandl 2003). It often forms dense clonal patches where native communities once existed (Moore 1975). Where herbivore pressure is present on neighbouring species, Canada thistle may also gain a competitive edge as its sharp spines deter herbivores (Nuzzo 1997).

Potential allelopathic properties

Many studies have shown that allelopathy can also be an important mechanism of interference by which Canada thistle may have harmful effects on neighbouring plant communities (Bendall 1975, Stachon and Zimdahl 1980, Kazinczi et al. 2001, Glinwood et al. 2004). Allelopathy is defined as the negative effect of one plant on another through the release of chemical compounds into the environment (Inderjit and Callaway 2003). Allelopathy is one form of non-resource based interactions among plants (Callaway 2002) and is distinguished from competition in that it entails the addition of a chemical to the environment, instead of the removal or reduction of some resource from the environment, of a neighboring plant (Hane et al. 2003). Allelochemicals are products of secondary metabolism and often act on target plants by retarding growth, inhibiting germination through disruption of cell division, interfering with respiration and other energy-transfer processes, or inhibiting nutrient uptake or translocation (Fisher 1980, Rice 1984). They may be released by volatilization (Glinwood et al. 2004), by leaching and exudation from the foliage, fruits, and roots (Fisher 1980), and/or by incorporation of litter into soil (Rice 1984). Allelopathy may contribute to the ability of particular exotic species to become highly invasive dominants in invaded plant communities and often to

establish virtual monocultures where diverse communities once flourished (Hierro and Callaway 2003).

Allelopathic effects of other species have been described as factors in the failure of tree regeneration (Gabriel 1975; Fisher et al. 1978; Fisher 1980; Mallik 1987, 1992; Hane et al. 2003; Skulman et al. 2004). However, most studies of allelopathy in Canada thistle have been in laboratory or greenhouse settings and have assessed impacts on crop species (Bendall 1975, Stachon and Zimdahl 1980, Wilson 1981, Kazinczi et al. 2004). Thus, it is yet unclear if allelopathy by this species can inhibit native trees under natural boreal forest conditions.

Difficulty to control or eradicate

The presence of Canada thistle infestations in GMNP is a concern because in agricultural and grassland landscapes, Canada thistle has proven very difficult to control and eradicate and often requires integrated mechanical, biological, and chemical methods of control (Trumble and Kok 1982, Donald 1990, Nuzzo 1997).

In agroecosystems, mechanical control (i.e. hand-cutting, mowing, digging, or tillage) is commonly used alone or in combination with various herbicide applications (Trumble and Kok 1982). Removal of thistle in this manner is often difficult due to the spreading root system that may extend to 2 m soil depth (Dock Gustavsson 1997). Selective cutting or mowing of aboveground biomass may be effective only when repeated at least three times each growing season for three to four years to decrease thistle fitness over time and eventually deplete root reserves (Nuzzo 1997, Zouhar 2001,

Hatcher and Melander 2003). These methods may be too time-consuming to be feasible for use within large infestations (Hutchinson 1992). Similarly, tiny fragments of root or subterranean stem tissue as small as 1 cm in length and 1 mm in diameter left behind after an eradication attempt or spread during soil tilling/cultivation are capable of supporting the emergence of new plants (Hamdoun 1972). The root fragmentation caused by tillage, as well as the creation of bare ground which is ideal for seedling establishment from the seed bank, may actually stimulate increased adventitious growth and a more severe infestation of Canada thistle (Heimann and Cussans 1996, Nuzzo 1997, Edwards et al. 2000).

At least eight insect species have been intentionally or unintentionally released in North America for biological control of Canada thistle (Maw 1976, Forsyth and Watson 1985, Nuzzo 1997). While a few of these introduced species cause conspicuous damage to individual plants (e.g. larvae of the dipteran fly *Orellia ruficauda* Fab., which damage seed heads), biocontrol currently provides little to no control of Canada thistle at the population level in North America (Moore 1975, Nuzzo 1997). Many biocontrol organisms released in North America are not adequately synchronized with Canada thistle's life cycle to cause significant mortality (Nuzzo 1997), and at least three biocontrol organisms may be needed for effective Canada thistle control in any area (Forsyth and Watson 1985).

A wide variety of herbicides have also been used in agricultural settings to control Canada thistle infestations (Nuzzo 1997, Grekul et al. 2005). Overall, systemic, nonselective post-emergent herbicides (e.g. glyphosate) have proven to be among the

most effective weapons against perennial weeds (Bradshaw et al. 1997). However, herbicides seldom provide long-term control of weeds when used alone and outside the context of an integrated weed management plan (Zouhar 2001). Moreover, use of chemical herbicides against Canada thistle is becoming increasingly unpopular, either because they are ineffective, uneconomic, or have harmful environmental effects (Edwards et al. 2000). Over-reliance on chemical control practices has exerted intense selection pressure on weed populations for rapid evolution of resistance to herbicides (Heap 2006, Smith et al. 2006) and herbicide-resistant biotypes of Canada thistle have been reported in Hungary and in Sweden (Solymosi et al. 1987).

Reviews of Canada thistle management strategies reveal the difficulty of eradicating and often even controlling Canada thistle populations and indicate a relative unpredictability of the species to these approaches (Trumble and Kok 1982, Donald 1990, Nuzzo 1997). Canada thistle is highly polymorphic and has numerous ecotypes that respond differently to control techniques (Nuzzo 1997). Additionally, the success or failure of any method is highly dependent on local factors such as habitat characteristics, soil conditions, and climate (Donald 1990).

Additional concerns with control in natural areas

Parks Canada policy states that "all practical efforts will be made to prevent the introduction of exotic plants and animals into national parks, and to eliminate or contain them where they already exist" (Minister of Supply and Services 1994). Yet controlling Canada thistle within a protected forest landscape, while minimizing damage to native

plants and encouraging the return of a native canopy, is predicted to be challenging and costly. There are currently no control or eradication methods for Canada thistle identified as suitable for widespread use in natural areas, and particularly not in boreal forests. Accumulating evidence suggests that implementation of invasive alien plant control efforts in natural areas are often unsuccessful and can have unexpected negative impacts on non-target native species and ecosystems (NRC 2000, Zavaleta et al. 2001, Smith et al. 2006). These impacts can be more severe than those caused by the non-native invader itself (Pearson and Callaway 2003, Messing and Wright 2006, Smith et al. 2006) and may lead to severe environmental degradation (NRC 2000). For example, conventional weed control in natural areas through chemical or mechanical means may open the door for further invasion as these practices create high rates of disturbance and resource availability (Hobbs and Humphries 1995, Smith et al. 2006). Smith et al. (2006) describe a mountain meadow in the northern Rocky Mountains that was treated with herbicide to remove the exotic invasive *Euphorbia esula* L. (i.e. leafy spurge) but resulted in the decimation of all exotic as well as native vegetation and the widespread invasive return of Canada thistle. Similar widespread use of herbicides in GMNP would kill many non-target native species and be a violation of Parks Canada policy to retain and restore ecological integrity in its National Parks (Mosquin 1997). Therefore, eradication of Canada thistle from boreal forest gaps, particularly where it is widely distributed and uncontained, is not likely a realistic management goal; Myers and Bazely (2003) point out that in such instances, complete eradication is not usually achievable even with massive economic investment. Rather, in light of the current regeneration failure

occurring within GMNP gaps and the linked relationship of alien plant invasion with hyperabundant moose populations, the problem may be best approached on a broader ecosystem scale (Noss 1996) before prematurely implementing an extensive, costly, and potentially ineffective thistle eradication program. Instead of focusing directly on methods of controlling Canada thistle, this research aims to identify potential effects of Canada thistle on forest regeneration processes and to explore the ability of open invaded gaps to support the growth of balsam fir and other native trees. Encouraging gap regeneration and a transition to a native forest canopy is a principal goal of Park managers, and the return to a more natural successional process in gaps may also phase out light-demanding Canada thistle populations over time.

Thesis objectives

This thesis had three major objectives:

Objective 1: The first objective was *to obtain a better understanding of the current conditions for regeneration and levels of invasion in forest gaps of GMNP.* Naturally and anthropogenically created gaps throughout the Park were surveyed and levels of balsam fir regeneration, levels of browsing on fir, occurrences of Canada thistle invasion of gaps, and the spatial extent of this invasion were determined. In addition, seedbed surveys were used to describe the percent cover of existing seedbeds in gaps, relate this information to their known suitability for supporting conifer recruitment, and assess the degree of seedbed degradation

caused by sustained disturbance pressure in gaps. This first objective is addressed in Chapter 2 and is vital to providing background information on the condition of gaps and setting the stage for all further experimental study.

Objective 2: The second objective was to use manipulative balsam fir seed-addition and seedling-addition experiments *to determine if balsam fir success (e.g. emergence, growth, and survival) is lowered within Canada thistle monocultures in forest gaps*, relative to areas of the gap not invaded by thistle as well as the adjacent, 'uninvaded' forest edge. This objective is addressed in Chapter 3. This chapter also discusses the potential mechanisms by which Canada thistle may affect balsam fir, compares fir success among disturbance regimes, and provides suggestions and recommendations for Park managers in GMNP.

Objective 3: The third objective was *to determine if Canada thistle can inhibit native boreal forest tree species through allelopathy*, and if allelopathy could potentially be a factor in regeneration failure. Two greenhouse experiments were performed to investigate the effects of Canada thistle extracts and soil residues on the emergence, survival, and growth of three dominant native tree species within eastern North American boreal forests: balsam fir, white spruce (*Picea glauca* (Moench) Voss), and white birch (*Betula papyrifera* Marsh). These experiments were designed to provide relevant information for forest management and address the role of allelopathy in possible restoration strategies

(e.g. whether residual soil allelopathy could limit tree re-establishment after removal of Canada thistle from an area). Allelopathy is the focus of Chapter 4.

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CO-AUTHORSHIP STATEMENT

All manuscripts in this thesis were co-authored with Dr. Luise Hermanutz. In all instances I was the principal contributor to project design and proposal, implementation of the field research component, analysis of the data and manuscript preparation.

Each of the three subsequent research chapters will be submitted as separate manuscripts for publication. Consequently, there is some necessary repetition between the general introduction and chapters.

2. Hyperabundant Moose in Gros Morne National Park: The Changing Face of the Boreal Forest Landscape

2.1. INTRODUCTION

Globally, and in a wide range of ecosystems, ungulate herbivores have demonstrated their capacity to fundamentally alter plant community composition, successional pathways, and ecosystem structure (Norton-Griffiths 1979; Crawley 1983; Coomes et al. 2003; Husheer et al. 2003; Rooney and Waller 2003; Weisberg and Bugmann 2003). Often, as a result of anthropogenic influences including land use changes, extirpations of native predators, protection from hunting, and exotic species introductions, many ungulate populations have undergone tremendous population increases in recent decades that have lead to catastrophic effects on native ecosystems (Weisberg and Bugmann 2003).

In many parts of the world, overabundant deer populations have restructured entire ecological communities via direct and indirect mechanisms (Rooney and Waller 2003) and have lead to cascading effects on native plant and animal species (Côté et al. 2004). Historically high white-tailed deer (*Odocoileus virginianus* Zimmerman) populations in the mixed conifer-hardwood forests around the Great Lakes in North America have limited the regeneration of preferred conifer (e.g. *Tsuga canadensis* (L.) Carr. and *Thuja occidentalis* L.) and deciduous (e.g. *Quercus rubra* L. and *Betula alleghaniensis* Britt.) tree species (Rooney and Waller 2003). In southern Ontario (Canada), including Point Pelee National Park, explosive deer populations have transformed heavily forested land into open grasslands (Mosquin 1997). Throughout

forests of central and southeastern Europe, deer browsing has been implicated in regeneration failure of European silver fir (*Abies alba* Mill.; Gill 1992; Motta 1996; Senn and Suter 2003).

Due to their evolutionary and geographic isolation, island ecosystems are often particularly vulnerable to ungulate introductions. For example, introduced deer have had severe impacts on community composition, forest regeneration, and ecosystems processes in New Zealand (Coomes et al. 2003; Husheer et al. 2003), Haida Gwaii (Queen Charlotte Islands, Canada; Stockton et al. 2005), Japan (Takatsuki 2009), and Anticosti Island (Canada; Potvin et al. 2003). As well, severe overbrowsing by moose (*Alces alces* L.) on Isle Royale (Michigan, U.S.A), following their colonization of the island in the early 1900's, lead to a drastically altered forest composition, a decline of favoured browse species, and canopy suppression of regenerating balsam fir (Risenhoover and Maass 1987; Brandner et al. 1990; McLaren and Peterson 1994). Moose are often termed 'keystone' species (Paine 1988) in the boreal forest due to their ability to greatly influence forest composition, processes, and structure when at high densities (Bergerud and Manuel 1968; Snyder and Janke 1976; Risenhoover and Maass 1987; Thompson et al. 1992; Pastor et al. 1993).

On the island of Newfoundland (Canada), introduced moose populations are known to reach densities that are ten-fold of that across much of their mainland range (Crête and Daigle 1999). Moose were introduced to Newfoundland in 1904 and rapidly colonized the island (Corbett 1995). The abundance of available forage, negligible competition from native herbivores (McLaren et al. 2004), and paucity of predation after

the extirpation of their primary predators, wolves (*Canis lupus* L.), in the 1930's (Pimlott 1959) provided ideal conditions for moose population increase. This increase has been further amplified within Gros Morne National Park (Island of Newfoundland, Canada; GMNP), a UNESCO World Heritage Site, where moose hunting has been prohibited since the Park's establishment in 1973. In GMNP, moose populations have increased from 0.14 moose/km^2 in 1971 to 5.0 moose/km^2 in preferred lowland forests during the latest 2007 survey (Burzynski et al. 2005; Thompson 2007). In the highest density survey units, densities were as high as 12.0 moose/km^2 in 2007 (Thompson 2007) and in the preceding 1998 survey, 4% of the Park area contained densities of 14.6 moose/km^2 (Burzynski et al. 2005). Moose in GMNP may be locally more numerous than in nearly any other recorded location in the world (McLaren et al. 2000).

Browsing by these overabundant moose populations is exerting extreme pressure on forests in GMNP (Rose and Hermanutz 2004) and having deleterious impacts on native species and forest structure (McLaren et al. 2004; Burzynski et al. 2005; Forbes 2006). Balsam fir (*Abies balsamea* (L.) Mill.), the most common and widespread tree species in GMNP, is failing to regenerate in many areas and is being maintained as a low, shrub-shaped tree by intense moose browsing. Unpalatable white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.) are avoided by moose and will likely replace fir as the dominant tree species (Forbes 2006). Many hardwoods are declining and disappearing from the canopy, including white birch (*Betula papyrifera* Marsh), which is the most abundant deciduous tree (Forbes 2006). Declines of other preferred browse species such as Canada yew (*Taxus canadensis* Marsh.), mountain

maple (*Acer spicatum* Lam.), *Amelanchier* spp., Northern wild raisin (*Viburnum cassinoides* L.), and American mountain-ash (*Sorbus americana* Marsh.) greatly reduce local species diversity (Bergerud and Manuel 1968; Corbett 1995; Lawlor and Methven 1995; Burzynski et al. 2005; Forbes 2006).

A primary concern of Park managers is the observed failure of lowland boreal forest gaps throughout GMNP to regenerate. As a result of sustained browsing pressure, gaps formed up to 30 years ago (i.e. since the late 1970's) as a result of natural (i.e. insect outbreaks) and anthropogenic (i.e. harvest) disturbance have still not returned to the expected closed canopy, balsam fir-dominated forest (Figure 2.1). Balsam fir is normally well adapted to regenerate after cycles of natural insect defoliations and small-scale harvesting. These disturbances favour the growth of the naturally established fir seedling bank, or 'advanced regeneration', which occurs under the mature forest canopy and is released from height suppression upon opening of the canopy (Hatcher 1960; Hall and Richardson 1973*a*; Osawa 1994; Duchesneau and Morin 1999). Regeneration from seedlings is crucial for fir regeneration after canopy loss because of the lack of a seed bank in this species (Frank and Safford 1970; Morin and Laprise 1997; Duchesneau and Morin 1999; Greene et al. 1999; Parent et al. 2003). However, balsam fir is a key component of the winter diet of moose (Des Meules 1962) and even before the onset of a gap-generating disturbance, moose heavily browse the advanced regeneration of balsam fir seedlings in the understory (Rose 2002). When disturbance occurs, moose concentrate their browsing activities in these early successional assemblages since they are re-vegetated with highly palatable species (Rose and Hermanutz 2004; Forbes 2006; Gosse

2006). Consequently, many sites are converting from closed boreal forest to an open landscape dominated by species unpalatable to moose (McLaren et al. 2004; Burzynski et al. 2005; Forbes 2006).

The lack of gap regeneration by balsam fir has encouraged the establishment of non-native plants in gaps disturbed by timber harvesting as well as insect infestations (Rose and Hermanutz 2004). It appears that moose are acting as conduits for the transport of alien plant propagules into remote forest sites and that they are also generating ideal conditions for alien plant establishment by maintaining conditions of disturbance and creating bare ground by trampling and destroying seedbeds (Burke and Grime 1996; Rose and Hermanutz 2004). In particular, concern has been generated by the presence of Canada thistle (*Cirsium arvense* (L.) Scop.) in some gaps (Rose 2002). Canada thistle is an introduced plant that is a serious noxious weed in grassland and agricultural landscapes (Moore 1975; Donald 1990). It has a very high vegetative and sexual reproductive capacity (Moore 1975; Nadeau and Vanden Born 1989; Heimann and Cussans 1996), allelopathic properties (Bendall 1975; Kazinczi et al. 2001; Glinwood et al. 2004), and is very difficult to control (Donald 1990). Throughout its range, Canada thistle has a tendency to become highly invasive, decrease native plant and animal species diversity, and alter natural ecosystem structure and composition (Nuzzo 1997). However, until now, this species has generally not been considered a major threat to boreal forests due to its high light requirements (Haber 1997).

Park managers are currently exploring options to encourage the return of these non-regenerating gaps to native forest and restore ecological integrity within GMNP.

However, little is yet known about the degree to which Canada thistle or other non-native invasive plant species have invaded boreal forest gaps of GMNP or how they impact seedbeds, a crucial determinant of early balsam fir establishment (Calogeropoulos et al. 2004). Similarly, the current state of regeneration within the gaps, the level of browsing on balsam fir therein, and the suitability of existing seedbeds for balsam fir regeneration based on knowledge of optimal seedbeds for conifer recruitment (McLaren and Janke 1996; Simard et al. 1998; Duchesneau and Morin 1999; Noel 2004), is largely unknown. As well, no data yet exist to determine how these properties may differ among natural and anthropogenic gaps. The first step towards developing efficient management strategies to encourage gap regeneration and eliminate invasive plant populations will be to gain a better understanding of the current condition of these forest gaps and the levels of natural regeneration associated with different disturbance types.

This study was designed to provide a better understanding of the existing conditions for native forest regeneration in boreal forest gaps shaped by a non-native, hyper-abundant moose population. In GMNP, transect and quadrat surveying techniques were used to sample forest gaps disturbed through either natural processes (i.e. insect infestations) or anthropogenic activities (i.e. small-scale harvesting). More specifically, the purposes of the study were to: 1) Describe the density of natural balsam fir regeneration in forest gaps and the degree of browse damage occurring on these individuals and determine whether the problems with forest regeneration are consistent among the two disturbance regimes; 2) Describe the spatial extent of Canada thistle invasion within gaps and determine if the degree of invasion differs among the two

disturbance regimes; and, 3) Describe the availability of favourable seedbeds for future conifer establishment within boreal forest gaps and to determine how seedbed quality in gaps differs: *a)* from that of the adjacent forest edge, where disturbance has not occurred, and *b)* among disturbance regimes.

2.2. METHODS

Study Area

This study was conducted in the boreal forest of Gros Morne National Park, located on the western coast of the Great Northern Peninsula on the Island of Newfoundland, Canada (49°30'N, 57°50'W). GMNP is a UNESCO World Heritage Site and eastern Canada's second largest national park at 1805 km². Gaps were surveyed in the lowland forest, which comprises 43% of the park's total area (Bouchard et al. 1991; Rose and Hermanutz 2004). These forests are composed predominantly of balsam fir mixed with white spruce and white birch; less abundant species include black spruce, trembling aspen (*Populus tremuloides* Michx.), and mountain maple. The coastal lowland forest region is characterized by cool summers (July mean: 15°C) and mild winters (February mean: -7.5°C) moderated by an oceanic influence, a short growing season of 140-150 days, strong prevailing southwesterly and westerly winds (Bouchard et al. 1991; Burzynski et al. 2005), and 1200-1450 mm of annual precipitation (Banfield and Jacobs 1998). Soils in the park are primarily humo-ferric podzols characterized by poorly drained acidic, mineral soils and formed under the influences of the parent material, humid climate, and coniferous vegetation (Clayton et al. 1977).

Field Research

In the summer of 2006, 24 disturbed forest gaps distributed widely throughout GMNP (Appendix I), and their undisturbed forest edges, were surveyed. Forest gaps were identified using GIS-indexed aerial photographs (ArcGIS version 9.1, ESRI Corporation, Redlands, California) obtained from Parks Canada as well as with the aid of local foresters. All chosen sites were originally fir dominated but deemed 'insufficiently restocked after disturbance' (Parks Canada, unpublished data). Gaps were chosen based on their predominant disturbance regime; 11 of the gaps were formed naturally by insect defoliators including eastern spruce budworm (*Choristoneura fumiferana* Clem.) and hemlock looper (*Lambdina fiscellaria fiscellaria* Guenee), and 13 gaps were formed by legal small-scale, traditional domestic harvesting by local residents. As part of the Federal-Provincial Agreement for GMNP, residents within the Park's seven enclave communities and two bordering communities are permitted to cut wood for personal uses within 12 Domestic Timber Harvest blocks comprising 129 km^2 of the 308 km^2 of lowland forest (Burzynski et al. 2005); all harvesting occurs during winter months when forests are snow-covered. In addition to disturbance regime, gaps were chosen based on their accessibility and distribution across the Park (Appendix I). Time since disturbance varied among gaps, with 17 of the gaps disturbed between 1977 and 1989, and 7 gaps formed from 1990 to 2004.

Regeneration survey

In June 2006, a continuous transect line was established along the longest axis through each forest gap as identified using GIS-indexed aerial photographs and field assessments; the size of the gap determined transect length and the number of quadrats surveyed. Along the length of each transect, 0.5 m^2 quadrats were taken at 5 m intervals. Nearly all fir within gaps were <1 m tall and it was not possible to classify balsam fir individuals as seedlings or saplings during the field survey because browsing damage made these designations unclear. Instead, to characterize the level of balsam fir regeneration and browse damage within forest gaps as well as the level of invasion by Canada thistle, within each quadrat the 1) density of balsam fir <30 cm in height, 2) density of balsam fir >30 cm in height, 3) presence or absence of apical meristem browse damage on these fir, and 4) density of Canada thistle shoots were recorded.

Seedbed survey

In August 2006, further surveys were performed in 19 of the identified forest gaps (10 natural, 9 anthropogenic) to characterize and quantify available seedbeds in gaps and their forest edges. In each gap, two 80 m transects were established: one was randomly positioned within the gap opening, and another established parallel within the adjacent forest edge. Eight $1m^2$ quadrats were established at 10m intervals along each transect line. Similar to methods used by McLaren and Janke (1996) and Noel (2004), within each quadrat the percent cover of all existing seedbed types at ground level (i.e. each substrate encountered on the forest floor) was estimated to the nearest 5% using a divided 1m × 1m

frame and grouped into one of 27 seedbed categories (e.g. coniferous litter, bare ground, hypnaceous mosses, exotic herbs; full list of seedbeds encountered are shown in Results section). In addition, all plant species within each quadrat was identified as either native or non-native and the total percent cover of all non-native herbaceous vegetation within each quadrat determined. Overall, seedbed cover was assessed in a total of 304 m^2.

Statistical Analyses

Regeneration survey

To determine if the density of regenerating balsam fir differed between natural and anthropogenic gaps, a one-way analysis of variance (ANOVA) was performed with disturbance regime as a fixed categorical factor (Proc GLM, SAS Institute, Cary, NC, USA). The analysis was performed on the density of all fir combined, as well as on the density of <30 cm fir seedlings only and >30 cm fir only. Analyses were Bonferroni corrected for three comparisons ($\alpha = 0.05$; α'(adjusted) = 0.017). All test assumptions for the analyses of variance were met as determined through examination of residuals for normality, homogeneity, and independence.

To determine if moose browse fir disproportionately among natural and anthropogenic gaps, logistic regression, a special case of the Generalized Linear Model for analyzing binary or proportional response data with categorical and/or continuous explanatory variables (Agresti 1996), was performed on SAS using a logit link (Proc GENMOD). Disturbance regime was considered a fixed, categorical factor. This analysis was also repeated on individual size categories of balsam fir (<30 cm and >30 cm), as

above. As another measure of balsam fir regeneration and distribution throughout gaps, logistic regression analyses were performed to determine if the number of quadrats containing balsam fir (all fir, <30 cm fir, or >30 cm fir), as a proportion of all quadrats sampled in each gap, differed among disturbance regimes. Similarly, a logistic regression analysis was performed to determine if the proportion of quadrats containing Canada thistle differed between natural and anthropogenic gaps. All logistic regression test assumptions were satisfied as determined through examination of residuals and model fit statistics. Where binomial models were overdispersed, a Pearson scale correction factor was applied (Littell et al. 2002). Additionally, a Pearson correlation was used to determine if there was a distributional relationship between balsam fir density and thistle shoot density within quadrats.

Seedbed survey

A Principal Component Analysis (PCA) using JMP 7.0.1 software (SAS Institute, Cary, NC, USA) was used to explore the ways in which seedbed types differ between gaps and forest edges, and among disturbance regimes. All quadrats were pooled (i.e. the locations from which sampling occurred were ignored) and a PCA was performed using a covariance matrix to determine if distinct clusters would emerge from the analysis and to separate the quadrats according to similar seedbed characteristics. In addition, a one-way ANOVA was performed in SAS (Proc GLM, SAS Institute, Cary, NC, USA) to determine if the percent of all exotic (i.e. non-native) herbaceous cover differed between natural and anthropogenic gaps. Percent data were arcsine square root transformed before

analysis to conform to model assumptions. Results were deemed statistically significant at $\alpha < 0.05$.

2.3. RESULTS

Regeneration Survey

The mean density of balsam fir regeneration occurring within boreal forest gaps of GMNP was 1.09 fir/m^2 in natural gaps and 0.91 fir/m^2 in anthropogenic gaps (Table 2.1). Levels of fir regeneration did not differ significantly among disturbance regimes (Table 2.1). Although fir size did not differ significantly between disturbance regimes, in natural gaps only 28% of individuals (i.e. 0.31 fir/m^2) were <30 cm in height whereas in anthropogenic gaps 64% of the fir (i.e. 0.59 fir/m^2) were <30 cm in height (Table 2.1). Fir >30 cm in height were recorded in a marginally significantly higher proportion of quadrats in natural gaps than in anthropogenic gaps (p=0.0190, Table 2.1). There was also no statistically significant difference (Table 2.1) in the spatial extent of fir between disturbance regimes. Of all 0.5 m^2 quadrats surveyed, only 28.8% in natural gaps and 22.2% in anthropogenic gaps contained balsam fir in any size category.

Regenerating fir had high levels of browse damage in both disturbance regimes (Table 2.1). Overall, the apical meristem was browsed in 91.8% of fir in natural gaps and 76.2% of fir in anthropogenic gaps; this difference in the levels of browsing between the disturbance regimes was marginally statistically significant (p=0.0421; Table 2.1). High proportions of smaller fir saplings (<30 cm in height) were browsed, with 78.9% and 69.4% of individuals browsed in natural and anthropogenic gaps, respectively (Table

2.1), but almost all taller fir (>30 cm in height) displayed browse damage on the apical meristem (98.3 % to 92.2%, respectively). Rates of browsing on these taller fir were marginally greater in natural gaps than in anthropogenic gaps (p=0.0488, Table 2.1).

On average across all gaps surveyed (n=24), Canada thistle was recorded in 5.0% of quadrats in natural gaps and 15.3% of quadrats in anthropogenic gaps; this difference among disturbance regimes was not statistically significant (p=0.1246, Table 2.1). Canada thistle was not found in every gap; it was recorded in 5/11 of the natural gaps surveyed (45.5%) and 5/13 of the surveyed anthropogenic gaps (38.5%). Re-analysis of how the spatial extent of Canada thistle invasion differs among disturbance regimes in *only* those sites in which Canada thistle was present revealed that Canada thistle invasion was not significantly more widespread, on average, within anthropogenic gaps (31.4% of quadrats) than in natural gaps (18.6% of quadrats; p=0.2124, Table 2.1), possibly reflecting the high variability in the spatial scale of invasion among individual gaps. Within those quadrats containing thistle, the mean (± SE) density of thistle shoots was 11.8 (± 1.64) shoots/m^2 and 10.3 (± 0.59) shoots/m^2 in natural and anthropogenic gaps, respectively. High thistle densities with maxima of 48 shoots/m^2 and 40 shoots/m^2 were recorded in each respective type of forest gap. In gaps containing Canada thistle, a slight negative correlation existed between densities of balsam fir and Canada thistle shoots (r = -0.086, p=0.0009).

Seedbed Survey

A PCA was used to determine if disturbance regimes or sampling locations (i.e. edge versus gap) could be separated based on seedbed characteristics. The first three principal components accounted for 43.9% of the variation (Table 2.2). Seedbed characteristics in forest gaps and their adjacent forest edges were distinctively different; a scatterplot of the first two components showed separation into two distinct clusters by PC2 (Figure 2.2). Forest edges were located primarily on the negative side of PC2, characterized by high negative loadings on hypnaceous mosses, mixed litter, coniferous litter, dicranaceous mosses, and *Cornus canadensis* L. (Table 2.2). Gaps were distributed primarily on the positive side of PC2 and which was characterized by high positive loadings on *Rubus* spp., exotic herbs, grasses/rushes/sedges, native herbs, and deciduous litter (Table 2.2). However, disturbance regimes did not separate across either PC1 or PC2, suggesting that seedbed characteristics within natural and anthropogenic gaps were quite similar, as were both their forest edge seedbeds (Figure 2.2). In addition to disturbance regime, neither location (i.e. gap or edge) or individual gap identities (data not shown) clustered around PC1; rather, this component was primarily driven by the presence or absence of native *C. canadensis* cover (-0.940) within the quadrat plot; overall, this small native plant was a common seedbed in gaps and edges in both disturbance regimes (Table 2.3).

Examination of a scatterplot of PC2 and PC3 again reveals the clear separation of gap seedbeds on the positive side of PC2 and edge seedbeds on the negative side of PC2 (Figure 2.3). In addition, it is evident that while forest edge seedbeds are not clustered

about PC3, gap seedbeds are clustered on the negative side of PC3. PC3 is characterized by a high positive loading on mixed litter seedbed (+0.848) and negative loadings on hypnaceous mosses (-0.436) and coniferous litter (-0.227) (Table 2.2). Therefore, while forest edges encompass these three seedbed types, gap seedbeds may be differentiated from forest edge seedbeds by a lack of mixed litter seedbed. Additionally, this plot of PC2 and PC3 portrays a lack of distinct clustering of gap disturbance regimes, again indicating the occurrence of similar seedbeds within natural and anthropogenic gaps (Figure 2.3).

The similarity in seedbed cover among natural and anthropogenic gaps was further made evident by examining a list of the most prevalent seedbeds available in each disturbance regime (Table 2.3). Both natural and anthropogenic gaps were dominated primarily by the same herbaceous vegetation: *C. canadensis,* grasses/rushes/sedges, other native herbs, *Rubus* spp., and non-native herbs. In both disturbance regimes, these categories comprised over 50% of the available seedbeds. The relative percent cover of these categories varied slightly among disturbance regimes: natural gaps contained a higher proportion of *C. canadensis* and grasses while anthropogenic gaps contained more non-native herbs and other native herbs (Table 2.3). There was also a greater presence of ferns (*Dryopteris* sp.) in natural gaps and bare ground in anthropogenic gaps. Since the seedbed survey was performed during August, plant growth was well developed in gaps and there was little bare ground (<5%). However, the area of bare ground was much greater in spring due to heavy trampling by moose on the wet soils remaining after snowmelt, which disturbs vegetated seedbeds and creates open ground that is rapidly

colonized by herbaceous ruderals (J. Humber, personal observation). Forest edge seedbeds were similar among disturbance regimes; both were dominated by hypnaceous mosses, *C. canadensis*, mixed litter, coniferous litter, and dicranaceous mosses (Table 2.3). Overall, these categories formed 66.1% and 72.9% of the seedbed in natural and anthropogenic forest edges, respectively.

The most common non-native herbaceous plant species recorded within forest gaps included Canada thistle, coltsfoot (*Tussilago farfara* L.), hawkweeds (*Hieracium spp.)*, buttercups (*Ranunculus repens* L., *R. acris* L.), and common dandelions (*Taraxacum officinale* Weber). A one-way ANOVA revealed that the percent cover of all non-native herbaceous vegetation combined was significantly greater in anthropogenic gaps than in natural gaps (anthropogenic: 16.5% ± 2.74%; natural: 9.6% ± 2.47%; $F_{1,150}$ = 4.10, p=0.0446).

2.4. DISCUSSION

Forest gaps throughout GMNP are experiencing forest regeneration failure. Balsam fir densities in natural (1.09 fir/m^2; i.e. 10,900 stems/ha) and anthropogenic (0.91 fir/m^2; i.e. 9,100 stems/ha) gaps are approximately two thirds less than 'normal' background levels of balsam fir regeneration that are expected for this region under lower moose densities. For example, during the 1970's when moose densities were lower (McLaren et al. 2004; Forbes 2006), Hall and Richardson (1973*b*) reported balsam fir seedling densities of 23,228 to 74,133 stems/ha in fir stands of western Newfoundland and Northern Peninsula forests at various periods after harvesting, with the norm being

regeneration densities well over 30,000 stems/ha. The fir regeneration densities for GMNP reported here are also lower than the range of fir seedling regeneration densities (14, 600 to 205,000 stems/ha, and an overall mean density of 80,118 stems/ha) reported for 14 balsam fir stands in Québec that were disturbed by spruce budworm outbreaks between 1974 to 1985 (Morin and Laprise 1997). Similarly, in a red spruce- balsam fir forest in New Hampshire, balsam fir regeneration was 8,000 to 53,000 stems/ha eight years after clearcutting and represented densities that were only 6-20% of the fir seedlings occurring in the adjacent intact forests (Hughes and Bechtel 1997). Levels of fir regeneration within GMNP are thus on the very low range of expected densities, and would be insufficient to adequately re-stock the forest gaps and eventually form a closed canopy.

Not only is the density of recruits too low to revegetate gaps in GMNP, but regenerating fir in gaps are experiencing extremely heavy browsing. Almost all fir >30cm in height had browse damage to apical meristems and even fir <30cm, which are often reported to escape from moose browsing (L. Hermanutz, unpublished data), were heavily browsed. Almost all of the browsed fir were stunted in appearance and contained multiple browsed leaders; the age of these individuals is unknown. Repeated browsing of apical buds and side branches can suppress fir height growth and recruitment into the canopy (Snyder and Janke 1976; Risenhoover and Maass 1987), halt transition from sapling to adults and thus decrease cone and seed production (Brandner et al. 1990; Noel 2004), and kill fir saplings (Bergerud and Manuel 1968). High levels of browsing on balsam fir in GMNP have been previously reported; Lawlor and Methven (1995) reported

that in 1993, 41.5% of available balsam fir stems were browsed on seral sites in GMNP. It is clear that moose browsing on established fir is a major factor preventing the natural regeneration of balsam fir forests in GMNP.

Problems of canopy replacement in GMNP may not be limited to low fir densities and high levels of browsing but may also involve the presence of unsuitable seedbeds for conifer recruitment within forest gaps. Since seedbed quality largely determines success of balsam fir at the germination and early establishment stages (Calogeropoulos et al. 2004), potential for future regeneration within gaps may be compromised. This may explain, in part, the low seedling densities found in gaps at GMNP. Seedbeds of natural and anthropogenic gaps were dominated primarily by dense native and non-native herbaceous vegetation and *Rubus* spp. shrubs. It is well known that dense herb communities disadvantage conifer regeneration because they compete for resources and the abundant leaf litter creates a barrier to the emergence and establishment of seedlings (Harvey and Bergeron 1989; Côté and Bélanger 1991; Coates et al. 1994; Kneeshaw and Bergeron 1996). Grass litter impedes the ability of seeds to contact the soil and makes them more prone to seed herbivory (Donath and Eckstein 2008). Similarly, shrub competition has been negatively correlated with the density of regenerating balsam fir in gaps (Batzer and Popp 1985; Morin and Laprise 1997). Greene et al. (1999) argue there is a narrow window of opportunity for post-disturbance conifer recruitment within harvested and burned forest gaps as optimal seedbed conditions rapidly deteriorate over time. For those reasons, our results suggest that even in the event of drastically lowered

moose populations, regeneration within gaps may not return to pre-moose densities and may require active restoration.

The potential for continued regeneration failure may be further heightened by the invasion of alien plants in boreal forest gaps of GMNP. This may be particularly true of anthropogenic gaps, where overall percent cover of herbaceous alien plants was highest. Several notorious non-native weeds, in particular, were identified in forest gaps: Canada thistle, coltsfoot, hawkweeds, buttercups, and common dandelions. Rose (2002) also identified these invaders as species of concern due to their ability to invade natural areas and, in the case of Canada thistle, coltsfoot, and *R. repens*, to form dense mono-specific patches. As well, Hendrickson (1999) emphasized the severity of the recent coltsfoot invasion throughout the Park and identified the anthropogenic and biogeographical factors mediating this species' invasive spread. It is unclear whether and how this suite of alien plants might deter the reestablishment of native trees. However, evidence from New Zealand suggests that in overbrowsed forests, the large numbers of introduced plants (e.g. exotic grasses) are likely to strongly impede reestablishment of native forest species independent of browsing pressure by introduced deer populations (Coomes et al. 2003).

This study suggests that the invasion of gaps by Canada thistle is widespread on a landscape scale throughout forest disturbances in GMNP, thus presenting a management challenge. Canada thistle was found to be present in close to half of all surveyed gaps in GMNP, and in these gaps, was distributed throughout 18.6% of sampled quadrats in natural gaps and 31.4% of quadrats in anthropogenic gaps at mean densities of 11.8 and 10.3 shoots/m^2, respectively. Maximum shoot densities in monocultures were 48

shoots/m^2. In light of the aforementioned potential threats posed by this alien invader, further study is required to determine if this species significantly threatens forest regeneration in GMNP.

Because low light availability, low nutrient availability, and low pH under closed canopy favour species with slow growing, nutrient-conservative life strategies and generally exclude alien plants with fast opportunistic growth strategies (Rose and Hermanutz 2004), alien plants are largely absent from the adjacent, undisturbed, closed forest edges. Forest edges are dominated by seedbeds more favourable for conifer establishment than open gaps, including hypnaceous mosses, *C. canadensis*, mixed litter, coniferous litter, dicranaceous mosses, and decaying wood (Côté and Bélanger 1991; McLaren and Janke 1996; Cornett et al. 1997; Simard et al. 1998; Duchesneau and Morin 1999). These seedbeds generally provide more stable moisture conditions and often, warmer microclimates (Parent et al. 2003). Initial survivorship of fir seedlings is thought to be inversely proportional to the depth of the organic layer and seedbed suitability can be ranked as: moss covered logs> moss> needle litter> broadleaf litter (Greene et al. 1999). Germination rates are generally higher on broadleaf litter than needle litter but subsequent survivorship is higher on needles (McLaren and Janke 1996); litter in GMNP forest edges was predominantly needles or a mixture of needle and <50% broadleaf litter. The abundant small native plant *C. canadensis* is also known to provide a very favourable seedbed for balsam fir regeneration in Newfoundland's boreal forests (Hall and Richardson 1973*b*; Burns and Honkala 1990). Poorer seedbeds such as rock, non-

decayed wood, and *Dryopteris* ferns (Duchesneau and Morin 1999) were recorded in low abundance within forest edges.

Overall differences between the anthropogenic and natural gaps surveyed were slight. Both disturbance regimes contained almost equally low densities of balsam fir regeneration and contained a very similar suite of gap and edge seedbeds, with only small differences in the relative availability of each seedbed. Levels of moose browsing on >30cm fir (i.e. >90%), and all fir combined (i.e. >75%), were extremely high in both disturbance regimes. Natural gaps contained a larger, although not significant, proportion of >30 cm fir while anthropogenic gaps primarily contained fir <30 cm in height. This height disparity was likely a result of more of the natural gaps surveyed having been disturbed at a slightly earlier date than most of the anthropogenic gaps; those gaps disturbed by insect outbreaks in the late 1970's, for example, may have started to regenerate before moose populations increased rapidly during the 1980's (McLaren et al. 2004; Forbes 2006). The spatial scale of Canada thistle invasion within gaps throughout the Park did not differ significantly between disturbance regimes, but the total % cover of all non-native plants was significantly higher within anthropogenic gaps as compared to natural gaps.

Management implications

Boreal forest gaps within GMNP are not regenerating to balsam fir forest. Rather, regeneration of disturbed forest throughout the Park's lowland areas has been stalled for up to 30 years, and the resultant open landscapes now more closely resemble weedy

fields than the natural forest ecosystem that Parks Canada aims to protect. Current densities of balsam fir within gaps will not be sufficient to eventually form a closed canopy forest. Sustained browsing pressure by overabundant moose, dramatically degraded seedbeds, and exotic plant invasion will likely continue to threaten the future of balsam fir regeneration within these disturbed forests. Declines in balsam fir as well as overall forest structure could also have cascading effects on numerous dependent native species, including birds (Setterington et al. 2000; Forbes 2006), specialist epiphytic tree lichens (Yetman 1999), and insects (Forbes 2006).

In GMNP, moose are an invasive introduced species that, if left uncontrolled, will continue to alter ecological integrity to a level that diminishes the ability of the Park to represent the natural region and maintain native biodiversity (Forbes 2006). Although Parks Canada's Guiding Principles and Operating Policies state that ecosystems should evolve in the absence of most human intervention, active management should occur to compensate for past human actions when maintenance or restoration of ecological integrity will be comprised without it (Parks Canada Agency 2000). A reduction in moose densities would have significant positive impacts on ecological integrity in GMNP (Forbes 2006), yet it is not known how conditions such as altered seedbed conditions and exotic plant invasion will affect forest regeneration or whether the existing open landscapes represent a shift to an alternate stable state (Noy-Meir 1975; May 1977) from which reversion will require active restoration (McLaren et al. 2009). Although trees suppressed for many years are sometimes capable of release from growth inhibition and recruitment into the canopy (Bergerud et al. 1968; Brandner et al. 1990), significant

changes to forest structure and functioning caused by sustained browsing pressure may not always be reversible and the altered ecosystems may continue to reflect the history of herbivory (Coomes et al. 2003). This has been exemplified in New Zealand, where control of invasive deer populations has not resulted in recovery of the original forest (Coomes et al. 2003). After four decades of red deer (*Cervus elaphus* L.) control in New Zealand and a population reduction of c. 92%, low remaining densities of introduced deer have been shown to restrict ecosystem recovery such that additional management strategies to encourage palatable plant species are required (Tanentzap et al. *in press*). Similarly, heavy reductions of white-tailed deer densities in Rondeau Provincial Park, Ontario (Canada) were not followed by return of the many native palatable understory species that have declined in this deciduous forest (Koh et al. 1996, Myers and Bazely 2003). Yet, combining a series of culls of white-tailed deer herds with active restoration of native plant communities (e.g. through reintroductions of native trees and shrubs) have been successful in reducing impacts of overgrazing on Carolinian forests in Point Pelee National Park and are gradually increasing regeneration of native herbaceous and shrub communities (McLachlan 1997, Buckley et al. 2008). Immediate action is needed in Gros Morne National Park to develop a strategy for active management and to uncover means of promoting stand regeneration within forest gaps.

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Table 2.1 – Results of a field survey of various conditions significant to regeneration of boreal forest gaps in Gros Morne National Park, NL, which were created by either natural or anthropogenic disturbance. The statistical significance (using ANOVA or logistic regression) of measured differences between disturbance regimes is shown at α (family-wise)=0.05. Descriptive measures include: the density of balsam fir (separated by height class), proportion of 0.5 m^2 quadrats containing fir, levels of apical meristem browsing on fir, and proportion of quadrats containing non-native Canada thistle.

Response	**Disturbance regime**		**Statistical significance**			
	Natural gaps (n=11)	Anthropogenic gaps (n=13)	F	χ^2	df	P
Total quadrats surveyed	764	1477				
Total area surveyed (m^2)	382.0	738.5				
Mean (SE) balsam fir density (m^{-2})						
<30 cm	0.31 (0.14)	0.59 (0.13)	2.06	-	1,22	0.1650
>30 cm	0.78 (0.21)	0.33 (0.19)	2.63	-	1,22	0.1190
Overall	1.09 (0.28)	0.91 (0.26)	0.22	-	1,22	0.6413
Mean (SE) proportion of quadrats containing fir						
<30 cm fir	0.135 (0.047)	0.151 (0.035)	-	0.07	1	0.7846
>30 cm	0.203 (0.048)	0.085 (0.024)	-	5.50	1	0.0190*
Overall	0.288 (0.068)	0.222 (0.045)	-	0.68	1	0.4102
Mean (SE) proportion of fir apically browsed						
<30 cm fir	0.789 (0.098)	0.694 (0.069)	-	0.58	1	0.4474
>30 cm	0.983 (0.012)	0.922 (0.033)	-	3.88	1	0.0488*
Overall	0.918 (0.043)	0.762 (0.061)	-	4.13	1	0.0421*
Mean (SE) proportion of quadrats with thistle						
All gaps combined	0.050 (0.039)	0.153 (0.047)	-	2.36	1	0.1246
Gaps with thistle only	0.186 (0.080)	0.314 (0.051)		1.56	1	0.2124

* Marginally significant (defined here as $p < 0.05$) after Bonferroni correction for three multiple comparisons (i.e. $\alpha = 0.05$; α' (adjusted) = 0.017).

Table 2.2 – Factor loadings on the first three principal components resulting from a PCA examining available seedbed cover in boreal forest gaps and their adjacent undisturbed forest edges in Gros Morne National Park, NL. Seedbed categories with the highest loading values on each principal component are indicated in bold face.

Seedbed	Loading on PC1 (17.6% of variance)	Loading on PC2 (14.3% of variance)	Loading on PC3 (12.0% of variance)
Hypnaceous moss	**0.211**	**-0.651**	**-0.436**
Dicranaceous moss	0.048	**-0.166**	**0.097**
Other bryophytes	0.006	-0.002	0.007
Decaying log[a]	0.044	-0.015	-0.064
Fresh log	0.019	0.049	-0.030
Standing snag	0.005	-0.004	0.004
Decaying stump[a]	0.015	-0.007	0.003
Fresh stump	0.001	0.016	-0.008
Deciduous litter	-0.037	**0.098**	-0.078
Coniferous litter	**0.099**	**-0.182**	**-0.227**
Mixed litter[b]	**0.119**	**-0.322**	**0.848**
Rock	0.012	0.005	-0.021
Bare ground	0.019	0.005	-0.038
Abies balsamea	-0.013	0.007	0.005
Picea spp.	0.000	0.002	0.002
Deciduous tree/shrub	0.001	-0.012	-0.006
Grass / rush / sedge	**0.126**	**0.254**	-0.066
Water	0.008	0.017	-0.003
Living root	0.002	-0.003	0.000
Rubus spp.	-0.006	**0.362**	0.027
Cornus canadensis	**-0.940**	**-0.114**	-0.030
Dryopteris sp.	-0.010	-0.003	0.086
Cirsium arvense	0.031	0.075	-0.013
Other native herbs	0.068	**0.250**	-0.034
Other non-native herb	**0.140**	**0.351**	-0.040
Mushroom	0.001	-0.001	0.000
Moose feces	0.002	-0.005	0.010

[a] Decaying wood (i.e. log or stump) was defined as wood that could be easily penetrated with a pencil.
[b] A mixture of coniferous and deciduous litter, normally with ≥ 50% coniferous content.

Table 2.3 – The 10 most abundant seedbed covers found in naturally- and anthropogenically- disturbed forest gaps, and their adjacent undisturbed forest edges, in lowland boreal forests of Gros Morne National Park, NL. Similarity among disturbance regimes between the top five most abundant gap and edge seedbeds is indicated by shading.

	Anthropogenic disturbance		**Natural disturbance**	
Location	Dominant seedbed	% Cover	Dominant seedbed	% Cover
Gap	Other native herbs	14.2	*C. canadensis*	16.4
	Rubus spp.	14.2	*Rubus* spp.	14.3
	Other non-native herbs	13.0	Grass / rush / sedge	10.4
	C. canadensis	10.5	Other native herbs	7.0
	Grass / rush / sedge	7.3	Other non-native herbs	6.9
	Deciduous litter	5.7	*Dryopteris* sp.	6.2
	Hypnaceous moss	5.2	Fresh log	6.0
	Bare ground	4.6	Decaying log[a]	5.2
	Decaying log[a]	4.5	Deciduous litter	5.0
	Fresh log	4.4	Hypnaceous moss	4.5
Forest Edge	Hypnaceous moss	23.2	*C. canadensis*	19.3
	Mixed litter[b]	16.7	Mixed litter[b]	16.0
	Coniferous litter	13.8	Hypnaceous moss	13.8
	C. canadensis	10.5	Coniferous litter	9.1
	Dicranaceous moss	8.7	Dicranaceous moss	7.9
	Decaying log[a]	7.1	Deciduous litter	7.5
	Bare ground	2.4	*Dryopteris* sp.	5.5
	Other native herbs	2.3	Other native herbs	4.1
	Decaying stump[a]	2.3	Decaying log[a]	3.8
	Rock	2.2	Fresh log	3.1

[a] Decaying wood (i.e. log or stump) was defined as wood that could be easily penetrated with a pencil.
[b] A mixture of coniferous and deciduous litter, normally with ≥ 50% coniferous content.

a)

b)

Figure 2.1 – Photographs from Gros Morne National Park in June 2006 of *a)* an anthropogenic gap disturbed by timber harvesting between 1980-1988, and *b)* a natural gap disturbed by an insect outbreak in 1977. Neither gap has regenerated to balsam fir forest, but instead remain open landscapes. Note that in *a)*, the only regenerating trees are widely spaced white spruce, which are unpalatable to moose. Yellow flowers in *b)* include exotic hawkweeds (*Hieracium spp.*) and dandelions (*Taraxacum officinale*).

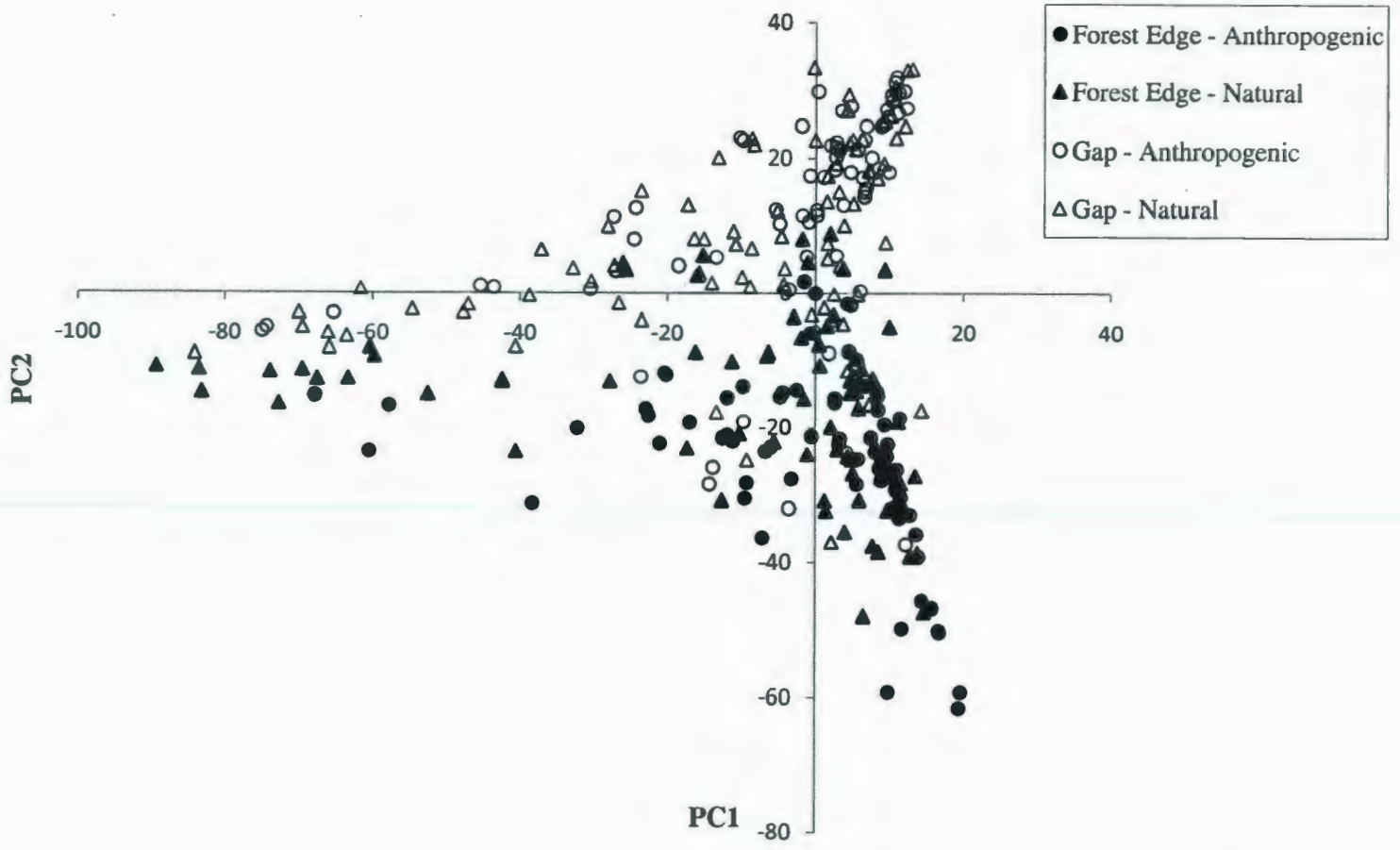

Figure 2.2 – Scatterplot of **Principal Component 1** (*x* axis) and **2** (*y* axis) from a PCA examining available seedbed cover in boreal forest gaps and their adjacent forest edges in Gros Morne National Park, NL. Each point represents a $1m^2$ quadrat, and points are coded according to their location (i.e. gap or forest edge) and disturbance regime (i.e. natural or anthropogenic). Combined, PC1 and PC2 accounted for 31.9% of the variation (17.6% and 14.3%, respectively).

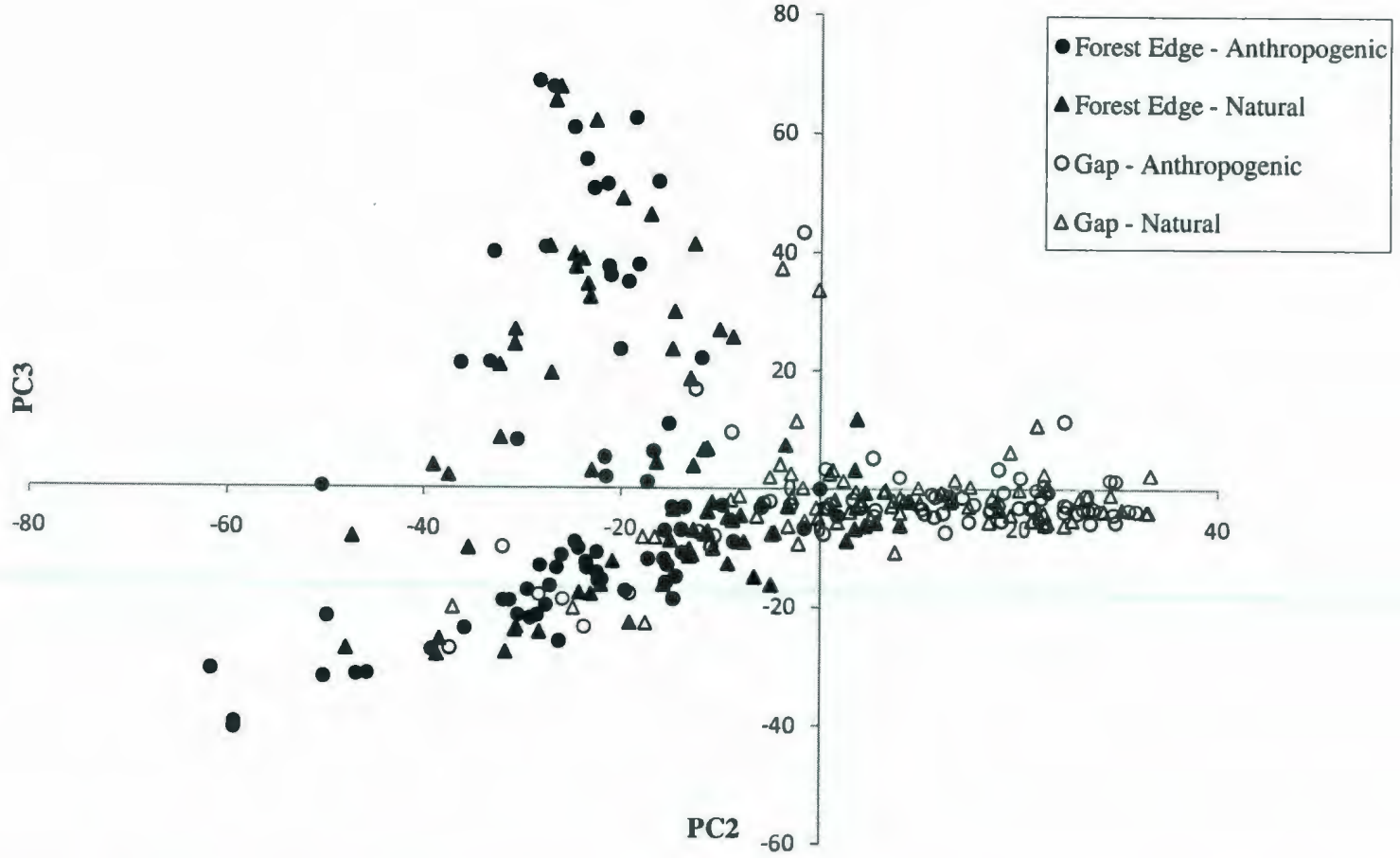

Figure 2.3 – Scatterplot of **Principal Component 2** (*x* axis) and **3** (*y* axis) from a PCA examining available seedbed cover in boreal forest gaps and their adjacent forest edges in Gros Morne National Park, NL. Each point represents a $1m^2$ quadrat, and points are coded according to their location (i.e. gap or forest edge) and disturbance regime (i.e. natural or anthropogenic). Combined, PC2 and PC3 accounted for 26.3% of the variation (14.3% and 12.0%, respectively).

3. Non-Native Plant Invasion and Hyperabundant Moose: Implications for Gap Regeneration in a Protected Boreal Forest

3.1. INTRODUCTION

Non-native plant invasions represent severe threats to native species diversity, ecosystem structure and function, and human welfare, both locally and on a global scale (Vitousek et al. 1997, Levine et al. 2003). With the increased rate of movement of species throughout the world and high rates of disturbance, non-native plants are becoming a larger component of regional floras and are prompting conservation concern by managers of protected areas worldwide (MacDonald et al. 1986, Cowie and Werner 1993, Myers and Bazely 2003, Rose and Hermanutz 2004). Developing a better understanding of the impacts of non-native species on the ecological integrity of protected areas (Parks Canada Agency 2000) and devising methods to reverse the effects of invasive species (Hobbs and Norton 1996, Zavaleta et al. 2001, Coomes et al. 2003) are increasingly recognized as imperative goals of conservation management.

In Canada's National Parks, alien plant species are considered the fourth most common stressor on ecological integrity (Canadian Heritage 1998). Many of the Parks contain hundreds of species of introduced plants (Mosquin 1997), yet, the large majority are found primarily in anthropogenically- disturbed areas such as roadsides, picnic areas, campgrounds, ditches, gravel pits, hiking trails, and other human-dominated areas (Mosquin 1997, Rose 2002). Many such alien plant species are relatively benign and do not invade, or have obvious negative impacts on, plant communities (Parks Canada Agency 2000, Myers and Bazely 2003). Typically, the greatest threat to ecosystem

functioning and native species diversity is posed when a non-native species becomes 'invasive' and successfully expands its range into natural or recovering protected ecosystems that are remote from human activity (Burke and Grime 1996, Mosquin 1997, Hendrickson et al. 2005, Rose and Hermanutz 2004).

However, when widespread invasion of sensitive areas does occur, controlling or eradicating the invader while minimizing damage to non-target native species and protecting surrounding natural communities can be a complex, and often impossible task (Myers and Bazely 2003). Accumulating evidence suggests that implementation of invasive alien plant control efforts in natural areas are often unsuccessful and can have unexpected negative impacts on non-target native species and ecosystems (NRC 2000, Zavaleta et al. 2001, Smith et al. 2006). In fact, impacts on native species diversity and ecosystem function by control and eradication practices can be more severe than impacts caused by the non-native invader itself (Hobbs and Humphries 1995, Matarczyk et al. 2002, Pearson and Callaway 2003, Messing and Wright 2006) and may lead to severe environmental degradation (NRC 2000) and further exotic invasions (Smith et al. 2006).

These are several of the issues now faced by managers of Gros Morne National Park of Canada (Newfoundand; GMNP) where Canada thistle (Compositae: *Cirsium arvense* (L.) Scop.), an herbaceous perennial alien plant in North America, has recently invaded widely-dispersed natural and anthropogenic boreal forest gaps on an extensive landscape scale. Surveys throughout the Park's vast area (1805 km^2) in 2005 indicated its presence in 55% of naturally-disturbed gaps and 41% of gaps formed by small-scale timber harvesting (Parks Canada, unpublished data) at densities up to 48 shoots/m^2

(Chapter 2). Many of these gaps are isolated within dense evergreen canopy and are often remotely located many kilometers from the nearest road. Canada thistle is well known as a problem invader in natural grassland communities where it is a serious threat to native species diversity (Mosquin 1997). It is also a common agricultural weed in field crops and in pasture land where it reduces crop yields and limits livestock grazing, costing millions of dollars in economic damage in southern Canada and the continental U.S. (Moore 1975, Donald 1990, Skinner et al. 2000). Despite its notoriety as a noxious weed in agricultural landscapes, its invasion into GMNP forests was not anticipated since Canada thistle has not generally been considered a threat to boreal forests (Haber 1997). Forests act as a relatively continuous barrier to wind dispersal of alien plant seeds (Brothers and Spingarn 1992) and the low light availability, soil pH, and nutrient availability in undisturbed forest canopies, which often separate gap openings by great distances, are unsuitable for growth of shade-intolerant herbs such as Canada thistle (Bakker 1960, Haber 1997, Rose 2002). However, it appears that Canada thistle invasion within GMNP has been facilitated directly and indirectly by extraordinarily high populations of non-native moose (*Alces alces* L.; Rose and Hermanutz 2004).

Since the Park's establishment in 1973 and the onset of protection from hunting, moose populations in GMNP have increased from 0.14 moose/km^2 in 1971 to densities of 5.0 moose/km^2 in preferred lowland forests during the latest 2007 survey (Burzynski et al. 2005, Thompson 2007). In the highest density survey units, densities were as high as 12.0 moose/km^2 in 2007 (Thompson 2007) and in the 1998 survey, 4% of the Park area contained densities of 14.6 moose/km^2 (Burzynski et al. 2005), revealing that moose in

GMNP may be locally more numerous than nearly any other recorded location in the world (McLaren et al. 2000). Browsing by these hyperabundant moose populations within GMNP's forests is having deleterious impacts on native tree species diversity and is threatening ecological integrity (McLaren et al. 2004, Burzynski et al. 2005, Forbes 2006). In winter, moose preferentially browse balsam fir (*Abies balsamea* (L.) Mill.), the dominant climax species in GMNP's forests and in all productive upland sites throughout western Newfoundland (Hall and Richardson 1973, Burzynski et al. 2005). Even before the onset of a gap-generating disturbance, moose heavily browse the advanced regeneration of balsam fir (Rose 2002). This advanced regeneration, or pre-established seedling bank, is balsam fir's primary means of restocking gaps after disturbance and is normally undisturbed in the understory after cycles of natural insect disturbance and small-scale harvesting remove the overstory (Hatcher 1960, Osawa 1994, Duchesneau and Morin 1999). The loss of the balsam fir seedling bank is highly detrimental to post-disturbance stand regeneration since balsam fir seeds do not form a persistent seed bank (Frank and Safford 1970, Morin and Laprise 1997, Greene et al. 1999). The moose-induced loss of the balsam fir seedling bank in GMNP is contributing to regeneration failure of naturally- and anthropogenically-created forest gaps. Densities of balsam fir seedlings within gaps are insufficient to restock forests (<1 individual per m^2; Chapter 2), and where young balsam fir does occur, it is highly stunted from sustained browsing pressure and is unable to reach adult reproductive stages or form a canopy (Chapter 2; also see Forbes 2006). Many recently disturbed sites have remained an open and

disturbed landscape and no longer provide typical structure for dependent wildlife (Burzynski et al. 2005, Forbes 2006).

Moose are, moreover, believed to facilitate and promote the invasion of non-regenerating gaps by alien plants such as Canada thistle by maintaining favourable conditions of disturbance over time. After canopy opening, moose maintain gap susceptibility to invasion by focusing their browsing on the highly palatable species that revegetate early successional stands (Rose and Hermanutz 2004, Forbes 2006, Gosse 2006). This activity maintains high light availability, and the trampling of native vegetation degrades seedbeds and creates competition-free sites by opening bare ground. These are ideal conditions for alien plant establishment (Burke and Grime 1996, Stohlgren et al. 1999, Rose and Hermanutz 2004). Rose and Hermanutz (2004) suggest that moose in GMNP also act as the primary conduits for alien seed dispersal (i.e. via mud on hooves and hair) into these favourable isolated habitat patches, as is evidenced by the frequent occurrence of alien plants along networks of moose trails throughout the Park (J. Humber, personal observation).

Canada thistle invasion into GMNP's protected forests has caused great concern among Park managers because of its known capacity for rapid growth, reproduction, and range expansion (Moore 1975, Nadeau and Vanden Born 1989, Donald 1994, Heimann and Cussans 1996), its superior competitive abilities (Robbins et al. 1970, Donald 1990), and the allelopathic potential of exudates from its shoots, leaves, and roots (Bendall 1975, Kazinczi et al. 2001, Glinwood et al. 2004). As well, in agricultural and grassland landscapes, Canada thistle has proven extremely difficult to control and eradicate because

of its deep, extensively spreading root network from which new clonal shoots readily arise (Hamdoun 1972, Dock Gustavsson 1997) and the long viability of its seeds in soil (Goss 1924). Furthermore, controlling widespread and uncontained Canada thistle populations within a protected forest landscape, while minimizing damage to native plants and encouraging the return of a native canopy, is predicted to be difficult. Myers and Bazely (2003) point out that in such instances, complete eradication is not usually achievable even with massive economic investment and thus is usually not a realistic management goal.

Instead of investigating costly and potentially ineffective and harmful methods of directly controlling Canada thistle in GMNP, this study takes a broader ecosystem-scale approach (Noss 1996) to management. The problem of Canada thistle invasion is deeply rooted in moose hyperabundance and the main goals of Park managers are to restore non-regenerating gaps to native closed-canopy forests and reestablish natural processes of regeneration and gap succession. Therefore, the primary goal of this study is to better understand if, and how, Canada thistle affects forest regeneration processes. It is unclear whether the accompanying widespread invasion of Canada thistle into open boreal forest gaps in GMNP will continue to impede the expected successional trajectory to a closed canopy forest should moose undergo an eventual population crash or, as is under consideration by Park managers, should human intervention be implemented to decrease moose populations and mitigate their impacts (McLaren et al. 2004, Forbes 2006, McLaren and Tom-Dery 2007). Under similar circumstances, Coomes et al. (2003) reveal that control of invasive deer populations in New Zealand have not resulted in recovery of

the original forest; rather, the altered ecosystems still reflect the history of herbivory and introduced plants (e.g. exotic grasses) continue to impede reestablishment of native forest species independent of deer populations. Because the herbaceous stratum of the forest understory represents one of the few potential barriers to tree regeneration, it can be viewed as an ecological filter to tree establishment which strongly influences the composition and structure of forests (George and Bazzaz 1999).

The second goal of this study was to determine if direct sowing of balsam fir seeds or planting of greenhouse-established fir seedlings would be successful in promoting native forest regeneration within gaps. Restoration of closed canopy forests in GMNP may require more effort than simply decreasing moose densities because natural balsam fir seedling recruitment in gaps is extremely low and seedbeds are presently dominated by unfavourable substrates for conifer recruitment, such as alien and native herbaceous weeds, grasses, and shrubs (Chapter 2). It is therefore likely that gaps will require active restoration. If, contrary to the hypotheses, balsam fir is capable of co-existing with Canada thistle, this would have important implications for forest management since shading by the regenerating tree canopy would likely eventually eliminate shade- intolerant alien herbs (Fisher 1987; Mosquin 1997). While this is beyond the scope of the present research, findings from these initial planting experiments will be valuable in identifying directions for future long-term study.

The third and final goal of this study was to determine how the success of balsam fir differs among gaps formed by natural or anthropogenic processes, as this knowledge

may identify how factors influencing forest regeneration vary among disturbance regimes and help guide management actions.

To achieve all three outlined objectives, both a balsam fir seed-addition and a seedling-addition experiment were performed in naturally and anthropogenically disturbed forest gaps within GMNP and success of this native conifer (i.e. emergence, growth, herbivory damage, and survival) was compared among regions of each gap invaded with thistle monocultures, areas not containing thistle growth, and the adjacent forest edge. To our knowledge, this is the first study to experimentally compare capabilities for native forest regeneration within adjacent areas concurrently containing or lacking an alien plant infestation. The purpose of this study was *not* to determine the causes for weed patchiness within gaps, i.e., if patchy distributions resulted from incomplete invasion or partial extinction within the gap, or if unoccupied habitat was unsuitable due to underlying environmental heterogeneities (Blumenthal and Jordan 2001). Rather, the goal was to better inform management decisions based on knowledge of fir success in thistle-invaded forest gaps. Because balsam fir establishment success was hypothesized to be limited within Canada thistle monocultures relative to uninvaded gap and forest edge areas, potential mechanisms by which Canada thistle might impede the establishment of balsam fir were also explored by comparing balsam fir success in unaltered Canada thistle monocultures to success in plots where only thistle shoots were removed. Aboveground competition for light and potential aboveground allelopathic effects from thistle shoots and leaves were excluded (Kazinczi et al. 2001) but any competitive or allelopathic interference by belowground root structures and/or potential

allelochemicals in soil were maintained. Since balsam fir is very shade tolerant (Hall and Richardson 1973, Burns and Honkala 1990), it was hypothesized that success of fir would not be improved significantly by removing thistle shoots alone. Additionally, fir success was compared to plots where all competitive and potential direct allelopathic interference was removed by eliminating above- and below-ground thistle biomass (Bendall 1975, Kazinczi et al. 2001) but retaining any residual toxicity in the soil. It was hypothesized that fir success would be improved in this treatment but would remain lower than in uninvaded areas since other studies of allelopathy in Canada thistle have demonstrated potential for residual soil to exclude neighboring vegetation (Bendall 1975, Stowe 1979, Wilson 1981).

3.2. METHODS

Study Area

This study was conducted in the boreal forest of Gros Morne National Park, located on the western coast of the Great Northern Peninsula on the island of Newfoundland, Canada (49°30'N, 57°50'W). GMNP is a UNESCO World Heritage Site and eastern Canada's second largest national park at 1805 km². The Park encompasses 69 km of coastline along the Gulf of St. Lawrence (Burzynski et al. 2005). Our research was restricted to lowland forests (<150 m elevation) which comprises 43% of the park's total area (Bouchard et al. 1991, Rose and Hermanutz 2004). These forests are dominated by balsam fir, white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), and white birch (*Betula papyrifera* Marsh). The coastal lowland forest

region is characterized by cool summers (July mean: 15°C) and mild winters (February mean: -7.5°C) moderated by an oceanic influence, a short growing season of 140-150 days, strong prevailing southwesterly and westerly winds (Bouchard et al. 1991, Burzynski et al. 2005), and 1200-1450 mm of annual precipitation (Banfield and Jacobs 1998). Soils in the park are primarily humo-ferric podzols characterized by poorly drained acidic, mineral soils and formed under the influences of the parent material, humid climate, and coniferous vegetation (Clayton et al. 1977).

All experiments were performed within 10 disturbed canopy gaps distributed widely throughout the Park's lowland forest (Table 3.1). Forest gaps were identified using time-sequenced GIS-indexed aerial photographs (ArcGIS version 9.1, ESRI Corporation, Redlands, California) obtained from Parks Canada as well as with the aid of local foresters. All chosen sites were originally fir-dominated but deemed 'insufficiently restocked after disturbance' (Parks Canada, unpublished data). Gaps were chosen based on their predominant disturbance regime: half of the gaps (n=5) were formed naturally by insect defoliators including eastern spruce budworm (*Choristoneura fumiferana* Clem.) and hemlock looper (*Lambdina fiscellaria fiscellaria* Guenee) and half were formed by legal small-scale, traditional domestic harvesting by local residents (i.e. anthropogenic disturbance). As part of the Federal-Provincial Agreement for GMNP, local residents within the Park's seven enclave communities and two bordering communities are permitted to cut wood for personal uses within 12 Domestic Timber Harvest blocks comprising 129 km^2 of the 308 km^2 of lowland forest (Burzynski et al. 2005). Time since disturbance varied among gaps (Table 3.1), with all gaps having been formed within the

past 30 years. Timber harvesting, or tree fall after succumbing to insect defoliation, often occurred over multiple years after the initial year of disturbance to eventually result in complete canopy removal. In addition to the predominant disturbance regime and time since disturbance, selection of sites was based upon the presence of Canada thistle monocultures (as determined during gap surveys in Chapter 2) as well as their accessibility (i.e. normally <1.5 km of a road, with the exception of SPA and SPB which were reached by boat; Table 3.1), approximate size of the gap, and distribution across the park.

Vegetation/seedbeds occurring within forest gaps are described in Chapter 2. The surrounding undisturbed forest canopies were composed predominantly of balsam fir mixed with some patchy white spruce and white birch; less abundant species included trembling aspen (*Populus tremuloides* Michx.), mountain maple (*Acer spicatum* Lam.), and black spruce. The ground vegetation in forests included a wide variety of herbs and mosses including *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not, *Hylocomium splendens* (Hedw.) B.S.G., *Rhytidiadelphus* sp., and *Dicranum* spp.

Seed addition experiment

In the first week of July 2006, five experimental plots (0.5m × 0.5m) were established within each forest gap (n=50 total plots) for addition of balsam fir seeds. Each plot was located within a specific region of the gap (noted below) and was considered a specific 'treatment' in which success of seed addition could be examined:

i) Canada thistle monoculture (T): Dense, unmanipulated Canada thistle monocultures with an average density of 30 shoots/m^2. At the time of planting, Canada thistle shoot height averaged 0.9 m among sites, although heights frequently reached >1.5 m later in the summer.

ii) Thistle monoculture with aboveground biomass removed ($T\text{-}_A$): Canada thistle monoculture as in i), but from which all aboveground Canada thistle biomass was removed by cutting shoots at soil level immediately prior to planting of balsam fir seeds and continually throughout the growing season at 10 day intervals.

iii) Thistle monoculture with above- and below-ground biomass removed ($T_{\text{-}AB}$): Both aboveground and belowground Canada thistle biomass were completely removed by digging up individual plants and their root systems from the soil immediately prior to planting balsam fir seeds; only aboveground thistle regrowth was subsequently cut at 10 day intervals to prevent damage to sensitive roots of balsam fir seedlings.

iv) Control – Uninvaded region of the gap (UG): A region within the gap that did not contain Canada thistle and was located at least 15 m from the nearest thistle plants. To minimize variability among gap replicates, this treatment was always established within a seedbed of *Cornus canadensis* L. (i.e. bunchberry), a native plant that is ubiquitous throughout the boreal forest, regularly co-occurs with balsam fir, and is known as a favourable seedbed for balsam fir establishment (Hall and Richardson 1973, Burns and Honkala 1990).

v) Control – Uninvaded forest edge (UE): A plot randomly established 5 m into the adjacent, uninvaded forest edge; this treatment was established as a control for the

gap itself, with which success of balsam fir seed addition in the UG treatment was compared.

Within a Canada thistle monoculture, the three plot locations for the T, T_A, and T_{AB} treatments (i-iii above) were randomly established within the same patch at a minimum separation of 1 m and treatment was assigned randomly to each plot.

Due to low local balsam fir seed crop and high pre-dispersal insect predation in the year prior to study, all seeds were obtained from the National Tree Seed Centre (NTSC), Canadian Forest Service (Fredericton, NB). Seeds were taken from trees in Bay D'Espoir, NL, and Roddickton, NL, and had documented germination rates of 50.0%. As per NTSC protocol, seeds were moist- stratified at 4°C for three weeks prior to planting; the documented germination rates were confirmed through controlled germination tests of seeds in environmental chambers. As the target was to establish and monitor up to 16 fir seedlings per plot, thirty-two balsam fir seeds (i.e. with 50% germination rates) were planted into each 0.5m × 0.5m plot by gently pushing them into the soil surface (n=1600 total seeds) immediately after plot preparation. Seeds were planted in pairs in a 4×4 grid, with 10cm spacing between each group of two seeds and a 10cm unplanted border on all sides. Immediately adjacent to each planted plot, an equally-sized (0.5m × 0.5m) unseeded control plot prepared in the same manner was established to quantify natural balsam fir emergence and establishment.

Throughout the first summer (2006), plots were surveyed for newly emerged seedlings at 10 day intervals. Overall emergence rates were based on detection of the shoot above the soil surface. The timing of seedling emergence was observed to closely

mimic the period of natural balsam fir emergence in the region. Newly-emerged seedlings were thinned to no more than one seedling per 10 cm × 10 cm area by clipping at the base of the stem, for a maximum remaining density of 16 seedlings per plot. At 10 day intervals, seedlings were monitored for survival and occurrence of browse damage until the end of the field season on 29 August 2006, at which time the season's growth had ceased and the terminal bud had set (Hanover 1980). At this time, height of remaining seedlings was determined to the nearest 0.001 cm. All seedlings were re-monitored during mid- June of 2007 and late May of 2008, or approximately one year and two years after planting, to track survival.

Seedling addition experiment

In mid-June of 2007, 432 balsam fir seedlings aged 15 months old were planted into four forest gaps within GMNP. Seedlings were obtained from Wooddale Provincial Tree Nursery, Newfoundland (Dept. of Natural Resources, Government of NL) and originated from balsam fir seeds collected from western Newfoundland. At planting, seedlings averaged 24.7 cm ± 0.2 cm (SE) in height. Gaps chosen for planting of seedlings were a subset of those having received seed addition. Two of the sites were naturally disturbed by insect outbreaks (i.e. SPB and BBA) and two were harvested sites (i.e. TKB and MBB; Table 3.1). Each gap contained multiple Canada thistle patches, together comprising approximately one third of the overall gap area. In each site, seedlings were planted into one of four locations corresponding to four of the seed-addition treatments (i, ii, iv, and v above), with the exception of the T_{-AB} treatment due to

limited seedling availability. Three replicate plots were established for each treatment and randomly positioned at a minimum separation of 1 m. Each plot measured 4 m × 4 m, with a 1 m unplanted border on all four edges and with nine seedlings planted in a 3 × 3 grid at a distance of 1 m apart on all sides. A total of 48 plots and 432 seedlings were established among the four sites. Each seedling was identified using a small metal tag pinned to the ground near the base of the stem. Change in seedling height (to 0.1 cm), change in basal diameter (to 0.001 cm), presence of browsing or desiccation damage, and mortality were monitored near the end of the first summer growing season (18-20 August 2007) and again in late May of 2008 after almost one year in the field to determine changes over the autumn-winter period.

Abiotic soil properties

Soil samples were collected for soil moisture determination from each of the 10 gaps on: 14-16 July 2006, 3-5 August 2006, and 23-25 August 2006; and from eight of the gaps on 13-15 June 2007 (two of the anthropogenic gaps could not be sampled at this time due to the presence of bears). In each gap, a $1m^2$ quadrat was randomly established in three treatments: Canada thistle monoculture (T), uninvaded gap (UG), and uninvaded edge (UE). Soil cores to 10cm depth were collected from the four corners of the quadrat and pooled in a tightly sealed sample bag at 4°C until laboratory procedures to determine percent soil moisture could be performed. At this time, pooled soil samples from each quadrat were thoroughly mixed and three subsamples of 10g ± 0.1g were removed,

weighed, and dried in a 70°C drying oven for 48 hours before reweighing. Percent soil moisture was calculated as:

$$\% \text{ soil moisture} = (\text{wet mass} - \text{dry mass}) / (\text{dry mass}) \times 100$$

Soil temperature at 10 cm depth was also determined in the eight gaps on 13-15 June 2007 using a Barnant (Type K) Themocouple Thermometer (Barnant Company, Barrington, IL). As in the soil moisture procedure, in each gap a $1m^2$ quadrat was randomly established within three treatments (i.e. T, UG, and UE) and soil temperature (°C) at 10cm depth was measured at each of the four corners of each quadrat. Soil moisture and temperature data were used to compare environmental conditions among treatments within each gap.

Statistical analyses

All statistical analyses were performed on SAS version 9.1 (SAS Institute, Cary, NC, USA) using generalized linear mixed modeling (GLMM; McCullagh and Nelder 1999). Where the response variable was a continuous variable with normal errors (i.e. height, basal diameter, soil moisture, or soil temperature), a mixed-model analysis of variance was performed using the MIXED procedure. All test assumptions were met as determined through examination of residuals for normality, homogeneity, and independence. In general, where the response variable consisted of binary or proportional data (i.e. proportion of seedlings emerging, surviving, sustaining browse damage, or desiccating), mixed-model logistic regression was implemented in the GLIMMIX procedure with a logit link and binomial errors. In comparison to the GLM and

GENMOD procedures (SAS Institute, Cary, NC, USA), respectively, the MIXED and GLIMMIX procedures have a comprehensive set of tools for working with random effects (Littell et al. 2002). The GLIMMIX procedure extends mixed models to incorporate non-normal errors (Littell et al. 2002).Variance components were estimated by restricted maximum likelihood (REML) in the MIXED procedure and residual pseudo-likelihood in the GLIMMIX procedure. Denominator degrees of freedom were calculated using the Satterthwaite approximation described in Fai and Cornelius (1996) except where repeated measures were incorporated into the model design, in which case the Kenward-Rogers approximation was used instead to avoid inflated Type I errors (Littell et al. 2002). These approximations often result in fractional degrees of freedom. Analyses were considered significant at $\alpha = 0.05$.

Seed addition experiment

The main model for the seed addition analyses consisted of both fixed and random categorical variables. Fixed factors included treatment (T, T_{-A}, T_{-AB}, UG, or UE), disturbance regime (natural or anthropogenic), and their interaction. The variable 'gap' (n=10) was nested within disturbance regime and treated as a random variable to account for variation among individual gaps. Due to the clustering of seeds/seedlings within small plot areas, the response of each individual within a plot may not be entirely independent (Littell et al. 2002). To handle the non-independence of repeated measures in space within a plot, 'plot identity' was included as a repeated effect (equivalently, a 'residual' or 'R-side' random effect in GLIMMIX) and specified a compound symmetric (i.e.

exchangeable) relationship among the individuals within a plot to account for correlated errors (Horton and Lipsitz 1999).

Overall balsam fir emergence was analyzed based on the proportion of viable seeds planted (i.e. 32 seeds × 50% viability = 16 viable seeds). Cumulative fir seedling survival was determined at three time periods: at the end of the first growing season (i.e. 'GS1'), at approximately one year (i.e. 'Y1'), and after about two years (i.e. 'Y2'). Survival of seedlings at each of these periods was expressed as the proportion of the total number of seedlings initially present in the plot (i.e. those remaining after post-emergence thinning). Fir survival was also determined between the first autumn-winter period (i.e. 'AW1', the period between GS1 and Y1) and between the first and second years (i.e. between Y1 and Y2); in these instances survival was based on the number of seedlings surviving in the previous life stage. Cumulative browsing damage on seedlings (including lethal and non-lethal damage) and analyses of seedling height were determined at the GS1 and Y1 stages.

When the effect of treatment was significant, *a priori* linear contrasts were used to compare means among selected treatments (Table 3.2) and Bonferroni corrected for four comparisons ($\alpha = 0.0125$).

Seedling addition experiment

Similar to the seed addition analyses, the seedling addition analyses included fixed variables for treatment (T, T_{-A}, UG, or UE), disturbance regime, and their interaction, as well as a random 'gap' variable nested within disturbance regime. A

second random variable accounted for treatment replication within any gap (n=3 plots per treatment) and was nested within gap. As well, each seedling within a plot was considered independent as it was widely separated from other individuals by at least 1 m on all sides. Cumulative fir seedling survival was analyzed at GS1 and Y1; autumn-winter survivorship between the GS1 and Y1 periods was also determined. Desiccation and browsing damage (lethal and non-lethal combined) as well as change in height and basal diameter since planting were analyzed at the GS1 and Y1 stages.

When the effect of treatment was significant, linear contrasts (Bonferroni corrected for three comparisons) were used to compare differences among selected treatments (Table 3.2).

Abiotic soil properties

Fixed factors in the analyses of soil moisture and temperature using the Proc MIXED procedure consisted of treatment (T, UG, or UE), disturbance regime, and their interaction. The variable 'gap' was again included as a random variable and nested within disturbance regime. In the analysis of soil moisture in 2006 , potentially correlated errors resulting from repeated measures over the field season were accounted for by adding 'sampling period' as a repeated effect with a first-order autoregressive structure to account for equal periods between re-sampling (Littell et al. 2002). Soil moisture was sampled once in 2007 and was analyzed separately.

When the effect of treatment was significant, linear contrasts were used to compare among pairs of means for each of the three treatments; alpha values were Bonferroni corrected for three comparisons ($\alpha' = 0.0167$).

In all analyses described above, where the interaction between treatment and disturbance regime was significant, the main effects could not be examined within this model (Sokal and Rohlf 1995) and thus the effect of 'treatment' was examined separately within each disturbance regime. For brevity, in the text we report only significant interaction terms. Results are expressed as mean ± standard error of the mean.

3.3. RESULTS

Seed Addition Experiment

Emergence

The effect of treatment on balsam fir emergence was determined separately within each disturbance regime due to a significant interaction ($F_{4,31.39}$=4.56, p=0.0051). In both anthropogenic and natural gaps, treatment had a significant effect on balsam fir emergence (harvested gaps: $F_{4,16.04}$=5.93, p=0.0040; natural gaps: $F_{4,15.14}$=5.40, p=0.0067). In the forest edges of harvested gaps, emergence of viable seeds averaged 27.5% ± 4.99%, yet within the gap openings the number of viable seeds emerging was extremely low, with no treatment in the gap having ≥ 10% emergence regardless of whether Canada thistle was present (Figure 3.1). Totaling all harvested gaps there was a total of only 2/80, 1/80, 8/80, and 2/80 viable seeds emerging in the T, T_{-A}, T_{-AB}, and UG treatments, respectively. Removing aboveground thistle biomass (T_{-A}) or both above- and

belowground thistle biomass (T_{-AB}) did not significantly improve emergence within thistle monocultures (p=0.6332 and p=0.1364, respectively; Figure 3.1). However, emergence in thistle monocultures were no lower than in areas of the gap not invaded by Canada thistle (p=1.0000). Only in the forest edge was emergence significantly improved over that in the gap (UE vs. UG; p=0.0066; Figure 3.1).

Balsam fir emergence was much higher in naturally-disturbed gaps than in harvested gaps (Figure 3.1). This difference was most notable in UG, where the mean emergence in naturally-disturbed gaps was 27.5 times higher than in anthropogenic gaps. Fir emergence within thistle monocultures (T) in natural gaps, although higher than the equivalent treatment in anthropogenic gaps, was only one third of the emergence in uninvaded areas (UG; p=0.0076). This high emergence in UG was significantly greater than in the UE (p=0.0084) treatment. Again, in natural gaps the fir emergence within Canada thistle monocultures was not significantly increased by removal of thistle biomass (T_{-A}: p=0.1113; T_{-AB}: p=0.1214); however, all emergence of balsam fir seedlings in thistle treatments (T, T_{-A}, T_{-AB}) occurred within just two of the five naturally-disturbed gaps (SPA and SPB; Table 3.1). No emergence occurred in T, T_{-A}, and T_{-AB} treatments in the other natural gaps.

Natural balsam fir emergence within all adjacent unseeded control plots was zero, thus emergence results reflect the outcome of seed addition, with no contribution from the resident seed bank.

Survival, browse damage, and height

By the end of the first growing season the two emerged seedlings in the T treatment and the one seedling within T_{-A} had succumbed to herbivory in the anthropogenic gaps. Only one of the two seedlings survived in the UG treatment. After two years, all of the surviving seedlings in the UG, T_{-AB}, and UE treatments had undergone mortality with the exception of one individual in T_{-AB} and one in UE, making two year survival rates in these treatments 16.7% and 5.6%, respectively. As a result of the extremely low initial emergence of viable balsam fir seeds within anthropogenic gaps, the impacts of Canada thistle monocultures on fir seedling survival, height, and browse damage could not be determined and were assessed only within the naturally disturbed gaps.

In naturally disturbed gaps, survival of newly emerged seedlings over the first summer growing season ranged from 32.6% to 72.2% among treatments (Figure 3.2). As previously noted, seedling survival rates in T, T_{-A}, and T_{-AB} are based on results from only two gaps since no emergence occurred in these treatments in three of the five gaps. The lowest survival was within the uninvaded gaps (UG) whereas the highest survival rates were in thistle monocultures (T) and were 2.25 times higher than in UG. In T_{-A} and T_{-AB} treatments, mean fir survival rates were also 1.62 and 1.80 times higher than in UG, respectively. By the following spring however (Y1), this pattern of higher survival within thistle areas was no longer evident (Figure 3.2). After two years in the field (Y2), no seedlings remained in any thistle treatment while 21.7% and 33.3% of seedlings were still

alive in UG and UE. However, none of these survival rates are statistically significant at α=0.05.

Herbivory on young seedlings was attributed primarily to voles because the stem was clipped cleanly; the remaining herbivory was attributed to slugs which leave characteristic slime trails. Herbivory was the main cause of mortality in the UG, UE, and T_{-AB} treatments. Because no trace could be found of 58.8% and 44.4% of the seedlings within the T and T_{-A} treatments, respectively, the cause of death was largely undetermined in these treatments (Figure 3.3). Desiccation was a minor cause of seedling mortality and occurred primarily within the T_{-AB} treatment. In the T treatment alone, 17.6% seedling deaths resulted from a wilting and curling of the upper shoot and needles that appeared unrelated to desiccation.

As in the analyses of seedling survival, there were no significant differences in height (GS1: $F_{4,3.53}$=2.13, p=0.2570; Y1: $F_{4,16.4}$=1.82, p=0.1723) or browse damage (lethal and non-lethal combined; GS1: $F_{4,5.272}$=0.43, p=0.7854; Y1: $F_{4,4.358}$=0.74, p=0.6069) among treatments in naturally disturbed gaps. Yet, examination of browsing patterns among treatments reveal that herbivory pressure was lower within T plots during the GS1 period than in all other treatments (Figure 3.4). Although browse damage in the three thistle treatments (T, T_{-A}, and T_{-AB}) increased during the first autumn-winter period (over which time Canada thistle shoots die back) while browse levels in UG and UE did not increase, by Y1 levels of browse damage still remained lower in T than in any other treatment within the gap opening (Figure 3.4).

Seedling Addition Experiment

Survival

After the GS1, AW1, and Y1 periods, there was no significant difference among treatments in the survival rates of transplanted balsam fir seedlings (Table 3.3). Relative to non-thistle treatments, survival of fir seedlings was never lower within thistle monocultures. Survival of balsam fir seedlings was very high over the first summer growing season; overall, only 7 of the 432 total seedlings (1.6%) experienced mortality. All but one of these recorded instances of mortality occurred within just one of the sites (SPB) and all were a result of desiccation. Survival was also high over the AW1 period and by the following May, after approximately one year in the field (i.e. by Y1), overall cumulative survival was 77.1% (i.e. 333/432 seedlings).

There were no significant differences in the survival rate of fir seedlings at Y1 between anthropogenic and natural gaps ($F_{1,2.024} = 0.46$, $p=0.5662$). There was a highly elevated mortality rate (by 2.6 to 4.5 times) in just one of the naturally-disturbed gaps (i.e. SPB) where atypically low soil moisture levels (Figure 3.5; Appendix II) apparently resulted in excessive seedling loss to desiccation. In all other sites, however, seedling survival was greater than 80% and almost all mortality was a result of either direct herbivory or uprooting by moose (Figure 3.5).

Desiccation

Only 27 of the 432 seedlings (6.3%) experienced lethal desiccation or partial desiccation (i.e. with some dead branches) by the end of their first summer in the field.

All but one of these instances of desiccation occurred within the insect-disturbed gaps, primarily within the SPB gap (n=21) but also within the BBA insect-disturbed gap (n=5) and this pattern appears to be related to lower soil moisture in these areas (Figure 3.5; Appendix II). The proportion of seedlings desiccating within insect-disturbed gaps over GS1 did not significantly differ among the four treatments ($F_{3,20}$=2.38, p=0.1004). Although not significant, the limited number of responses suggests a slight pattern of lower desiccation within T and T_{-A} treatment plots during this period (Figure 3.6).

By the end of the first year in the field (Y1), cumulative desiccation was 18.1% (78/432 seedlings). Again, desiccation was a factor only within the insect-disturbed gaps (n=77/78 of the cases), with almost all instances of desiccation occurring within the SPB gap (n=68) and a much smaller proportion within BBA (n=9). In these natural insect-disturbed gaps, desiccation differed significantly among treatments ($F_{3,20}$=3.55, p=0.0331), with most desiccation occurring within the open uninvaded areas of the gaps (Figure 3.6). Desiccation in UG was significantly higher than in the forest edge (1.86 times higher, p=0.0073) and marginally higher than in thistle monocultures within the gap (1.63 times higher, p=0.0207). Removing thistle shoot biomass did not significantly affect the level of fir seedling desiccation (p=0.2075).

Herbivory

All herbivory on transplanted balsam fir seedlings was attributed to moose browsing. Browse damage on seedlings by moose was low during the first summer in the field, with only 5.8% (25/432) of seedlings browsed. Due to the low number of

responses, the statistical model outlined could not be applied. Although limited, the responses (Figure 3.7) indicate that browsing was 3.3 to 5.0 times higher in areas within the gap and forest edge lacking thistle than in the T and T_{-A} treatments, respectively.

Moose herbivory on seedlings greatly increased over the fall and winter, and by late May (Y1), 49.5% (214/432) of seedlings had been browsed by moose. Browse damage was disproportionate among treatments at Y1 ($F_{3,40}$=8.96, p=0.0001), with seedlings in the forest edge having 1.49 times more browse damage than those in uninvaded regions of the gap (p=0.0009). Levels of herbivory in thistle monocultures did not differ from those in UG (p=0.2069), and removing thistle shoots did not significantly influence herbivory damage (p=0.6650; Figure 3.7). There was no difference in herbivory between anthropogenically and naturally disturbed gaps (dist: $F_{1,2.001}$=0.16, p=0.7266).

Growth

The effect of treatment on fir height growth after the first summer growing season (GS1) was determined separately within each disturbance regime due to a significant interaction term (Table 3.4). In anthropogenic gaps, change in seedling height after planting differed significantly amongst treatments (p<0.0001; Figure 3.8*a*; Table 3.5), with seedlings in the T treatment gaining significantly more height than those in UG and T_{-A} plots. There was no difference in seedling height growth between UG and UE treatments (Table 3.5). In natural gaps, the differences in seedling height growth amongst treatments was only marginally significant (p=0.0711, Table 3.5) although seedlings in thistle monocultures experienced nearly double the height growth of seedlings in UG and

UE treatments (1.83 and 1.91 times more, respectively; Figure 3.8*a*). Removing thistle shoots did not affect seedling heights as it did in anthropogenic gaps (Figure 3.8*a*). In all treatments except T_{-A}, the height growth of seedlings over GS1 in the naturally-formed gaps was less than half the increase in height in the harvested gaps (Figure 3.8*a*).

Although the above analyses of seedling height change over GS1 reflect the actual fate of seedlings planted in the field, and are thus valuable for management purposes, they include seedlings that may have experienced decreases in height from moose browsing and therefore height differences reflect not only direct consequences of growing within its particular treatment but also incorporate the differential level of herbivory among treatments. Excluding browsed seedlings from the above analyses yielded similar results over GS1 (Figure 3.8*b*, Tables 3.4-3.5), since browse damage was minimal during this period, but greatly changed observed height growth patterns over the first year (Y1; Table 3.4; Figure 3.9). Over the first year, there was no difference in seedling height growth among disturbance regimes when all seedlings were included ($p=0.6691$) or when browsed seedlings were excluded from the analysis ($p=0.2681$). When all seedlings were included in the analysis for year 1, the effect of treatment on height change was significant ($p=0.0204$, Table 3.4). However, seedlings experienced a decrease in height in all treatments (0.46 - 2.81 cm loss; Figure 3.9) due to high levels of moose browsing over the autumn and winter periods (Figure 3.7). The only significant *a priori* contrast (Table 3.2) was between T and UG ($p=0.0052$), with seedlings in T treatments experiencing the least height loss overall (Figure 3.9). The actual heights of balsam fir seedlings after Y1, averaged across all treatments and disturbance regimes,

was 23.04 cm ± 0.37 cm. Re-analysis of only unbrowsed seedlings better reflects height growth over the Y1 period (Figure 3.9). Mean height growth ranged from 1.45 to 2.41cm but did not differ significantly among treatments ($p = 0.1603$; Table 3.4). Although not significant, most growth occurred in the T treatment. After this first year in the field, the actual mean height of all the unbrowsed seedlings only, averaged across treatments and disturbance regimes, was 25.97 cm ± 0.34 cm.

There were, with one exception, no significant effects of treatment or disturbance regime on balsam fir basal diameter growth during any time period; basal diameter growth of (unbrowsed) fir seedlings differed significantly amongst treatments in natural gaps only during the GS1 period (treatment*disturbance: $F_{3,389}=3.12$, $p=0.0261$; anthropogenic gaps: $F_{3,198}=0.85$, $p=0.4677$; natural gaps: $F_{3,190}=6.94$, $p=0.0002$). During this time the growth in basal diameter of seedlings in the UG treatment (0.559 ± 0.082 cm) was significantly greater than seedlings in T (0.281 ± 0.075 cm; $p=0.0057$) and UE (0.092 ± 0.069 cm; $p<0.0001$) treatments. Removing aboveground thistle shoots did not significantly affect basal diameter of fir seedlings growing amongst Canada thistle (T_{-A}: 0.328 ± 0.079 cm; $p = 0.5380$).

Abiotic Parameters

In 2006, soil moisture levels at seedling rooting depth did not differ among treatments ($F_{2,42.2}=0.36$, $p=0.7023$) but there was a significant difference in percent soil moisture content among disturbance regimes ($F_{1,7.9}=9.33$, $p=0.0159$). Soil of naturally disturbed gaps was considerably drier than anthropogenic gaps (natural: 1.24 ± 0.42%

moisture; anthropogenic: 3.06 ± 0.42%). This pattern of low soil moisture was consistent throughout the natural gaps and *not* solely driven by exceedingly low soil moistures within SPB (and neighboring SPA) alone; with one exception (RBA), soil moisture content was higher in all anthropogenic gaps than in natural gaps (Appendix II). In 2007, soil moisture levels in each treatment was determined separately for each disturbance regime due to a significant interaction ($F_{2,57.1}$=8.72, p=0.0005). In anthropogenic gaps, there were slight differences among treatments ($F_{2,22}$=3.37, p=0.0531), with % soil moisture content in T (3.26 ± 0.49%) marginally higher than in UE (2.79 ± 0.49%; p=0.0290) and UG (2.83 ± 0.49%; p=0.0432) treatments. In natural gaps, soil moisture content among treatments was significantly different ($F_{2,35.5}$=14.38, p<0.0001) with the highest moisture levels in UE (1.72 ± 0.28%), less moisture in T (1.10 ± 0.27%), and very low moisture levels in UG (0.51 ± 0.27 %); all treatments were significantly different at $\alpha' = 0.0167$ (Bonferroni-corrected). In 2007, soil in the five natural gaps was generally drier than the anthropogenic gaps (Appendix II).

Soil temperature at 10 cm depth, as measured during the 2007 growing season, was significantly different among treatments ($F_{2,64.4}$=44.22, p<0.0001) but not among disturbance regimes ($F_{1,5.37}$=0.00, p=0.9702). Soil temperatures in T (13.65 ± 0.33°C) were significantly higher than temperatures in UG (12.61 ± 0.33°C; p=0.0008) and UE (10.78 ± 0.34°C, p<0.0001).

3.4. DISCUSSION

Invasion of non-native Canada thistle into boreal forest gaps negatively affects balsam fir regenerative processes at early stages of emergence and survival, and thus may continue to impede natural balsam fir regeneration independent of future moose densities. However, the success of balsam fir within Canada thistle-invaded boreal forest gaps is dependent upon numerous factors including the life stage in which fir is planted (i.e. as seeds or seedlings), the way in which success is measured (i.e. emergence, survival, growth), the history of forest disturbance, and the distinctive abiotic conditions specific to individual gaps. In particular, older seedlings transplanted into Canada thistle patches were not disadvantaged over the first year and thus may be a viable management strategy to encourage regeneration in invaded gaps.

Seedling emergence, growth, and survival

The most evident effect on balsam fir germinating amongst thistle monocultures was significantly lowered emergence. In natural gaps there was a strong pattern of decreased balsam fir emergence within thistle monocultures as compared to uninvaded areas of the gap, where emergence was three times higher. Herbaceous Canada thistle cover could potentially act as an ecological filter capable of shaping community composition by influencing tree species emergence abilities, as George and Bazzaz (1999) describe for the fern understory in New England forests. In the present study, physical removal of either aboveground Canada thistle biomass (i.e. by cutting shoots) or both above- and below-ground Canada thistle biomass (i.e. by digging up entire plants)

did not improve emergence. This suggests that the presence of Canada thistle in gaps severely limits natural recruitment of fir from seed and that this effect is not a result of direct competition from Canada thistle, but may be largely through allelopathic or other effects within soil (Bendall 1975, Stowe 1979, Wilson 1981). From a management perspective, it is instructive to note that these two treatments also simulated, on a smaller scale, frequently employed methods of mechanical thistle control in small infestations (i.e. hand cutting or mowing, and digging up, respectively; Trumble and Kok 1982, Donald 1990, Dock Gustavsson 1997); thus, suggesting that such management treatments used to control Canada thistle do not improve the chances of successful balsam fir emergence and establishment. However, in anthropogenic gaps the impact of Canada thistle on fir success was less obvious because fir emergence was ubiquitously low (usually <2.5%) throughout all regions of the gap. This research therefore highlights a serious problem with recruitment limitation throughout anthropogenic gaps, whether invaded by thistle or not.

All subsequent statistical analyses that were based on the success of these balsam fir germinants in natural gaps (i.e. browse damage, survival, height) were severely limited in their ability to detect a treatment effect, since results in all three thistle treatments (T, $T_{\cdot A}$, and $T_{\cdot AB}$) could be based on seedlings monitored in two of the five gaps only. In many cases, lack of statistical significance may have been partially or entirely a product of highly disproportionate initial emergence within just two of the natural gaps. In addition, the statistical models used were conservative since they incorporated random variables to account for seedling clustering within plots. For these reasons, the biological

significance of experimental outcomes must also be incorporated into interpretations of the results of seed addition experiments.

Results from natural gaps suggest that survival of fir seedlings successfully emerging among Canada thistle is low over the first two years but initially, after the first growing season and the first year, fir survival within thistle monocultures does not differ from the other treatments. In the first year, balsam fir seedlings were not disadvantaged when growing within Canada thistle monocultures as this exotic invader frequently afforded some positive influences on its native neighbors. In particular, those new fir seedlings that were able to emerge within thistle monocultures in natural gaps experienced less than one fifth of the level of browsing, and had over 2.25 times the survival rate, than seedlings in uninvaded areas of the gap during their first growing season. This finding is biologically significant since conifer seedlings are at greatest risk of predation during the first 10-16 weeks post-germination (Duchesneau and Morin 1999, Noel 2004). During the growing season, the sharp spines on Canada thistle apparently deterred herbivores and offered protection to neighboring fir from early seedling consumers. Removal of aboveground, or above- and belowground, thistle biomass was not beneficial as it caused increases in the level of browsing on fir and thus decreased survival. During the autumn-winter period, Canada thistle shoots die back and likely offer less protection to fir: browsing incidence on seedlings in all three thistle treatments (T, T_{-A}, and T_{-AB}) increased during this period but damage remained the lowest in the thistle monoculture (T) after one year. This facilitative effect was unexpected although similar positive interactions between neighboring plants occurring under conditions of strong

consumer pressure have been elsewhere described (Bertness and Callaway 1994, Brooker et al. 2008).

However, after two years in the field no seedlings remained in any thistle treatment while 22% of seedlings survived in uninvaded areas of the gap (UG) and 33% remained in the surrounding uninvaded forest edge (UE). A tradeoff may exist for newly emerged seedlings growing amongst thistle: there may be a net benefit on seedlings at early stages when the seedling is most vulnerable to herbivory, but over time, negative influences on survival could outweigh any benefits. This steady decline in survival over two years in the thistle-invaded areas differs from patterns in uninvaded areas of the gap and the forest edge, where initial seedlings losses were the greatest during the first few months, but declined only minimally thereafter. It is expected that further losses of remaining seedlings in these two uninvaded treatments will be minimal, since seedling population losses are usually minor after the first few years of growth (Burns and Honkala 1990, Simard et al. 2003).

For all seedlings in both disturbance regimes, herbivory by small mammals and slugs was the main cause of mortality in uninvaded treatments (UG and UE) as well as in the entire thistle biomass removal treatment (T_{-AB}); at least 80% of deaths in these treatments could be unequivocally attributed to either herbivory or desiccation. However, in unaltered thistle monocultures (T) and where thistle shoots were removed (T_{-A}), a larger proportion of seedlings (58.8% and 44.4%, respectively) disappeared without a trace and thus cause of death could not be determined. In these instances, it is not clear if the entire seedling was consumed, or rather, if mortality was a direct result of competitive

or allelopathic influences of Canada thistle; the decaying remains of these tiny seedlings could have been difficult to recognize during re-monitoring after the autumn-winter period. The seedlings may have been buried and smothered by senescing Canada thistle shoots in autumn, or their survivorship may have been disadvantaged over time by growing under dense cover (Duchesneau and Morin 1999). In the thistle monoculture (T) treatment alone, 17.6% of seedlings died from a curling over and wilting of the seedling from the top (symptoms that appeared unrelated to desiccation as seen in other treatments where the seedlings had dried upright and experienced colour change to a brown or reddish hue). These findings could potentially point to an allelopathic effect of Canada thistle on balsam fir and highlight the importance of further studies on this potential mechanism of interaction between the species.

Transplanted seedlings

All of the larger transplanted nursery-derived seedlings experienced low levels of browsing over the first growing season (5.8%) as they were not preyed upon by small mammals and slugs, which are responsible for high rates of herbivory on new emergents (Noel 2004). They also largely avoided moose herbivory until the autumn-winter period, when moose begin to rely heavily on balsam fir (Des Meules 1962) and browsing levels increased. Moreover, there was some evidence of thistle protecting these older fir seedlings from herbivory, as browsing damage over the first growing season was 3.3 to 5.0 times higher in the uninvaded gap (UG) and uninvaded forest edge (UE) treatments, respectively, than in thistle monocultures.

In fact, over the duration of one year, there was no evidence of any negative impact of transplanting nursery-derived balsam fir seedlings (aged 15 months at planting) into thistle monocultures as success was no lower among thistle than in uninvaded regions of the gap or the surrounding forest edge. Fir survival did not differ among treatments and overall, seedling additions were very successful, with 77% of all seedlings surviving the first year in the field and most of the mortality attributed to desiccation within just one gap (i.e. SPB). Excluding this gap, average survival among treatments was 86%. Levels of desiccation were lower, and percent soil moisture contents higher, in thistle-invaded areas of the gap than in native gap vegetation. It is possible that Canada thistle favoured moister soil conditions within forest gaps, although moisture is not normally a major limiting factor for this species and it commonly grows in very dry soil such as sand dunes and sandy fields (Moore 1975, Nuzzo 1997). Most likely, the microclimate created by the dense herbaceous thistle canopy may have helped to prevent soil drying; balsam fir survival is usually higher under partial to full cover because the canopy shelters seedlings from temperature extremes and soil desiccation (McLaren and Janke 1996, Duchesneau and Morin 1999, Calogeropoulos et al. 2004). Monitoring at the end of the first year in the field revealed slightly increased fir desiccation within plots where aboveground thistle biomass was removed. There were also slight benefits of thistle with regard to height growth of the transplanted fir seedlings after the first growing season and the first year. It is possible that the dense Canada thistle growth provided additional nutrient resources to fir through canopy leaching (Brooker et al. 2008). Alternatively, fir seedlings may have allocated more resources to height growth than

diameter to overcome strong competition for light under thistle. This latter explanation may be less likely since balsam fir basal diameter was significantly lower in thistle monocultures than uninvaded gaps in only one instance (i.e. after the first growing season in natural gaps).

The results suggest that older, nursery-derived balsam fir seedlings are capable of growing among dense Canada thistle monocultures without experiencing significant consequences to survival or growth. In fact, removal of aboveground thistle shoots by cutting appeared to be slightly disadvantageous to fir seedling success. However, as the success of these transplanted seedlings could be followed for only one year, it is not certain whether these benefits will persist. Allelopathic effects of other plant species can cause the failure of tree regeneration (Fisher 1987). For this reason, it is important to better understand the potential allelopathic interactions between Canada thistle and native boreal tree species (Chapter 4).

Effect of disturbance regime and gap variability

This study revealed that success of balsam fir emergence and establishment frequently differs greatly between disturbance regimes as well as among individual gaps. Balsam fir emergence was very poor in native uninvaded seedbeds of anthropogenic gaps but not those of natural gaps. Yet, survival of the transplanted nursery seedlings was no lower in anthropogenic gaps than in natural gaps. In fact, these older seedlings experienced elevated levels of desiccation in natural gaps (i.e. particularly in the SPB gap) while dessication was not an issue in anthropogenic gaps. As well, fir seedlings

transplanted into anthropogenic gaps experienced approximately double the height growth of seedlings in natural gaps in all but one treatment (T_{-A}) during the first growing season. The significantly lower percent soil moisture content in natural gaps (Appendix II) potentially explains the decreased growth and increased desiccation of older, transplanted fir seedlings in natural gaps, but does not explain the decreased fir emergence in the generally moister soil of anthropogenic gaps considering that moisture is the most limiting factor to balsam fir germination (Burns and Honkala 1990). Since seedlings were always planted within a consistent seedbed within the gap (i.e. either within a favourable native seedbed of *Cornus canadensis*, or within a thistle monoculture), seedbed variation does not likely explain the observed differences. Previous research has shown that while gap seedbed communities differ from those in forest edges, seedbed quality and dominant plant communities are very similar among insect-disturbed gaps and harvested gaps (Chapter 2). Further research is needed to investigate if the ubiquitously low amount of emergence within anthropogenic gaps may potentially be the result of higher levels of seed predation in this disturbance regime (Simon et al. 1998, Sullivan et al. 1999), as remnants of predated seeds were occasionally observed within experimental plots. Future study should also be focused towards determining which edaphic or other environmental factors are driving the decreased soil moisture levels within natural gaps in GMNP.

The success of balsam fir and the effect of treatment also varied among individual gaps. This is exemplified by the two most northerly and anomalous natural gaps studied: SPA (i.e. seed addition) and SPB (i.e. seed and seedling additions), which are closely

located in the Northern Peninsula Ecoregion (Table 3.1). In the seed addition experiment, these two gaps were the only naturally disturbed sites in which there was any fir emergence within patches of Canada thistle (T, T_{-A}, and T_{-AB} treatments). However, in the seedling addition experiment, transplanted seedlings in SPB experienced relatively high rates of mortality from desiccation compared to the second natural gap (BBA) and the two anthropogenic gaps. Seedling mortality from desiccation in SPB was likely due to its location on a south-facing ridge which, in winter, is frequently wind-swept and may be susceptible to deep or late frosts as it experiences less snow accumulation than surrounding areas (Tom Knight, Parks Canada, personal communication, 2007). This factor combined with the lack of rainfall in the region for 20 consecutive days in the spring of 2008 (17 April – 6 May; Environment Canada 2009) may have attributed to increased seedling desiccation within this gap. Because disturbance regime received little replication in the seedling addition experiment (i.e. two gaps per disturbance type), individual gaps played a large role in driving observed patterns among the regimes. All statistical models used incorporated this high gap variability into probability determinations by including a random variable for gap and also accounted for any correlation between clustered individuals within a plot. Yet the results highlight the extreme variability among sites and suggest that the response of balsam fir to thistle invasion is complex and highly dependent upon individual gap characteristics. For these reasons, any restoration program that targets individual gaps for direct sowing of seeds or plantings of tree seedlings would greatly benefit from an initial, detailed evaluation of the suitability of local environmental conditions. As well, small-scale trials to evaluate

success of a planting program within the specific gaps to be targeted may be advantageous to identify potential pitfalls before making large financial investments.

Additional impacts on regeneration in non-regenerating gaps

This study has emphasized the interrelated impacts of Canada thistle invasion and hyperabundant moose populations, yet the results also suggest that GMNP's ecological integrity may be further threatened by yet other non-native species. Sixty-five percent of early seedling mortality over the first two years was directly attributable to herbivory by small mammals and slugs; and, this rate may be greatly underestimated since another 27.1% of the seedlings disappeared without leaving evidence of the cause of mortality. The only native small herbivorous mammal in Newfoundland is the meadow vole (*Microtus pennsylvanicus terranovae* Bangs), whereas a host of non-native mammals have invaded the island including the snowshoe hare (*Lepus americanus* Erxleben), masked shrew (*Sorex cinereus* Kerr), deer mouse (*Peromyscus maniculatus* Wagner), red squirrel (*Tamiasciurus hudsonicus* Erxleben), eastern chipmunk (*Tamias striatus* L.), and most recently, the redback vole (*Clethrionomys gapperi* Vigors) (Noel 2004, Burzynski et al. 2005, Kasimos 2006). In a 2001 survey, 91% of all small mammal captures in the forest of Gros Morne were non-native species (Burzynski et al. 2005). Newfoundland also contains at least 10 species of established slugs (*Arion* spp., *Limax* spp., and *Deroceras* spp.) and all but one species (*Deroceras laeve* Müller) is non-native (John E. Maunder and Ronald G. Noseworthy, personal communication, 2007). Small mammals and slugs are voracious consumers of newly emerged tree seedlings (Nystrand and

Granström 1997, Côté *et al.*, 2005) and threaten balsam fir at an earlier stage than moose (Noel 2004). Since the synergistic effects of numerous non-native species can lead to cascading effects on native species in island ecosystems (Fritts and Rodda 1998), further study is needed to better understand the potential additive role of these non-native animals in preventing regeneration in Gros Morne National Park's balsam fir forests.

Management implications

Augmenting Canada thistle- invaded anthropogenic forest gaps of GMNP with balsam fir seeds is not a viable approach to encouraging regeneration due to extremely low emergence. Although emergence was much more successful in natural gaps, sowing is likely still an inefficient management approach because of high rates of loss to early seedling mortality, negative impacts of Canada thistle on emergence and survival, and unpredictable success among gaps. Moreover, the sowing protocol involved individually planting seeds at a favourable position slightly under the soil surface, yet large-scale restoration normally involves either broadcast sowing, hydro-seeding, or in very large-scale projects, aerial seeding from low-flying aircraft (Davy 2008). Also, when planting fir seeds within uninvaded regions of gaps, selective planting was performed within a consistent favourable seedbed (i.e. *C. canadensis*), yet actual large-scale sowing for restoration purposes would, by necessity, be much less selective and previous research indicates that the majority of seedbeds existing within these gaps are unfavourable for conifer recruitment (Chapter 2). For these same reasons, the results suggest that even in the event of significantly decreased moose densities, non-regenerating boreal forest gaps

in GMNP (especially those disturbed by timber harvesting) are not likely to regenerate on their own from seed.

Where barriers to the success of sown seeds exist, restoration processes may be greatly accelerated by the planting of more mature plants to rapidly reestablish populations of important or keystone species (Davy 2008). Because such methods are labour-intensive and potentially expensive, they are most suitable for long-lived perennial species with a distinctive role in the ecosystem (Davy 2008), such as balsam fir. The results of this study indicate that planting greenhouse-established seedlings could be a viable approach to actively promoting native forest regeneration and natural successional processes within gaps, regardless of whether they are invaded by Canada thistle or not. Such an ecosystem approach to management, where ecosystems are the conservation targets rather than individual species (Noss 1996), may be much more effective in this system than targeting control efforts towards Canada thistle alone since the problem of invasion is rooted in large-scale changes to ecosystem processes and disturbance regimes (Chapin et al. 2000, Myers and Bazely 2003). It is essential that restoration projects be founded on realistic and achievable goals (Hobbs and Norton 1996, Simberloff 1998, Coomes et al. 2003).

Even if single-species control of Canada thistle is desired, any attempts at achieving and maintaining this control in large or widespread infestations may not be feasible or financially realistic (Mosquin 1997, Rejmánek and Pitcairn 2002, Smith et al. 2006). As well, aggressive chemical or mechanical weed control in protected natural areas can threaten sensitive non-target native species and stimulate further alien plant

invasion (Hobbs and Humphries 1995, Zimdahl 2004, Smith et al. 2006). By shifting the management focus towards re-establishing a native forest canopy, control of non-native ruderal plants may also be achieved as they are shaded out over time. Canada thistle is highly shade intolerant: its growth is considerably reduced in 60-70% of full daylight levels (Bakker 1960) and early canopy closure, even by seedlings of species considered inferior competitors, can greatly reduce its vigour (Trumble and Kok 1982, Donald 1990, Edwards et al. 2000). Mosquin (1997) suggests that shade- intolerant alien herbs can often be eliminated by encouraging the development of a full native tree canopy overhead; this has been successfully practiced in abandoned farmland and old fields in eastern Canada to form dense closed conifer canopies which shade out alien grasses and forbs over many years (Fisher 1987, Mosquin 1997). This less 'invasive' option to combat large or widespread invasive weed populations holds great potential for the management of sensitive natural areas. In Gros Morne National Park, long-term monitoring will be necessary to determine if infestations of Canada thistle can be combated with a successional approach.

Ultimately however, no restoration program initiated to encourage balsam fir regeneration and canopy formation in Gros Morne National Park will be successful unless moose densities are first lowered. Although there were no negative impacts of Canada thistle on transplanted fir seedlings over their first year, seedlings in all treatments within both forest gaps and in edges underwent very high levels of moose herbivory and experienced significant height suppression. The nursery-grown balsam fir seedlings planted had undergone some fertilization during early greenhouse production

and thus could have been more susceptible to moose herbivory than naturally-established fir seedlings due to potentially higher nitrogen content (Mitchell and Hosley 1936, Tripler et al. 2002); however, other research in Gros Morne National Park has clearly shown that naturally regenerating balsam fir also experience extreme rates of browsing by moose (Chapter 2; see also Lawlor and Methven 1995 and Forbes 2006). Allocating valuable resources towards gap regeneration will be futile as long as moose continue to suppress canopy development; similarly, any attempts to control or prevent Canada thistle invasions will be unsuccessful in the long term if the root cause of the invasion remains. Restoration actions that combine moose reductions with a planting program to restore natural regenerative processes (McLaren et al. 2009) may be the best first step for managers of Gros Morne National Park. In Point Pelee National Park (Canada), culling of hyperabundant white-tailed deer herds combined with reintroductions of mid-successional trees and shrubs, passive restoration (i.e. encouraging natural colonization), and modifications to topography and hydrology have allowed for reductions in impacts of overgrazing on Carolinian forests and are gradually increasing regeneration of native herb and shrub communities and shading out non-native ruderal plants in some areas (McLachlan 1997, Buckley et al. 2008). Until the overabundant moose population is lowered in Gros Morne National Park, either naturally or through human intervention, these charismatic non-native animals will remain the greatest inhibitors to forest regeneration and will continue to redefine the community compositions of this protected forest landscape.

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Table 3.1 – Characteristics of 10 boreal forest gaps studied in Gros Morne National Park, NL. Gaps are identified here by abbreviations only; complete names of each gap are found in Appendix I.

	Natural gaps					Anthropogenic gaps				
	BBA*	SPA	SPB*	WWB	LOB	MBA	MBB*	TKB*	RBA	RBB
Major disturbance type	Insect	Insect	Insect	Insect	Insect	Harvest	Harvest	Harvest	Harvest	Harvest
Period of disturbance	1987	1977	1977	1987	1987	1987	1983	1997	2000	1996
Distance from road (m)	605	6580	6732	854	1241	613	735	653	100	100
UTM (NAD 83) (East/North)	432989 / 5497845	449086 / 5521623	449277 / 5521735	454507 / 5474005	443585 / 5479048	443513 / 5483778	443623 / 5483859	443665 / 5483379	447116 / 5481694	447275 / 5481575
Elevation (m)	76	75	77	35	34	77	99	56	69	66

* Gaps in which both seed-addition and seedling addition experiments were performed

Table 3.2 – *A priori* contrasts performed to compare specific treatment means upon the finding of a significant treatment effect in seed and seedling addition experiments. Contrasts were Bonferroni corrected for multiple comparisons (Seed addition: α'=0.0125; Seedling addition α'=0.0167).

***A priori* questions**	**Contrast[a]**	**Seed addition**	**Seedling addition**
1. Does balsam fir success differ between regions of a gap either invaded or not invaded by Canada thistle?	T vs. UG	✓	✓
2. Does removing aboveground Canada thistle biomass affect balsam fir success?	T vs. T_{-A}	✓	✓
3. Does removing above- and below-ground Canada thistle biomass affect balsam fir success?	T vs. T_{-AB}	✓	
4. Does balsam fir success differ between the uninvaded gap regions and the uninvaded forest edge?	UG vs. UE	✓	✓

[a] Treatment abbreviations: T = Canada thistle monoculture, T_{-A} = thistle monoculture with aboveground shoot biomass removed, UG = uninvaded region of the gap, and UE = uninvaded forest edge.

Table 3.3 – Mean proportion of balsam fir seedlings surviving after various periods of time following transplant into four field treatments in boreal forest gaps of Gros Morne National Park, NL. Results of mixed-model logistic regressions indicating statistical significance among treatment means are shown. Due to the very low mortality over GS1, inferential statistics could not be performed.

Period of seedling survival	Mean (SE) by treatment[a]				Mixed-model logistic regression		
	T	T_{-A}	UG	UE	F	df	p
GS1: Cumulative survival over first growing season	0.991 (0.009)	0.991 (0.009)	0.963 (0.018)	0.991 (0.009)	---	---	---
AW1: Autumn-winter survivorship	0.804 (0.038)	0.785 (0.040)	0.740 (0.043)	0.804 (0.038)	0.79	3, 40	0.5055
Y1: Cumulative first year survivorship	0.796 (0.039)	0.778 (0.040)	0.713 (0.044)	0.796 (0.039)	1.12	3, 40	0.3533

[a] Treatment abbreviations: T = Canada thistle monoculture, T_{-A} = thistle monoculture with aboveground shoot biomass removed, UG = uninvaded region of the gap, and UE = uninvaded forest edge.

Table 3.4 – Statistical results of mixed-model ANOVAs indicating the fixed effects of treatment, disturbance regime, and their interaction on change in balsam fir seedling height during the first growing season (GS1) and first year (Y1) after transplant into boreal forest gaps in Gros Morne National Park, NL. Statistical results are compared among analyses that included all seedlings and analyses that excluded seedlings damaged by browsing. Results were deemed significant at $\alpha < 0.05$ (bold face).

Time Period	Variable	All seedlings			Browsed seedlings excluded		
		df	F	p	df	F	p
GS1	Treatment	3, 406	4.93	**0.0023**	3, 382	4.19	**0.0062**
	Dist.Regime	1, 2	3.97	0.1847	1, 2	3.55	0.2001
	Treatment*Dist.	3, 406	4.60	**0.0035**	3, 382	7.72	**<0.0001**
Y1	Treatment	3, 317	3.31	**0.0204**	3, 185	1.74	0.1603
	Dist. Regime	1, 2.02	0.25	0.6691	1, 1.91	2.38	0.2681
	Treatment*Dist.	3, 317	2.03	0.1100	3, 185	1.16	0.3254

Table 3.5 – Statistical results of mixed-model ANOVAs comparing the effect of treatment in which seedlings were transplanted on change in balsam fir seedling height over the first summer growing season (GS1) within natural and anthropogenic boreal forest gaps in Gros Morne National Park. Statistical results are compared among analyses that included all seedlings and analyses that excluded seedlings damaged by browsing. Where the effect of treatment is significant at $\alpha < 0.05$, results of *a priori* contrasts are shown. Significant contrasts after Bonferroni correction are displayed in bold face.

	All seedlings							Unbrowsed seedlings only						
	Difference among treatments?			*A priori* contrasts[a]				Difference among treatments?			*A priori* contrasts[a]			
	df	F	p	T – T_A	T – UG	UG – UE	T – UE	df	F	p	T – T_A	T – UG	UG – UE	T – UE
Disturbance														
Anthropogenic	3, 210	7.64	**<.0001**	**<.0001**	**0.0106**	0.2550	0.1552	3, 198	8.16	**<.0001**	**<.0001**	0.0313	0.3618	0.2245
Natural	3, 200	2.38	0.0711	--	--	--	--	3, 187	3.61	**0.0144**	0.7289	0.0865	0.5408	**0.0163**

[a] Treatment abbreviations: T = Canada thistle monoculture, T_A = thistle monoculture with aboveground shoot biomass removed, UG = uninvaded region of the gap, and UE = uninvaded forest edge.

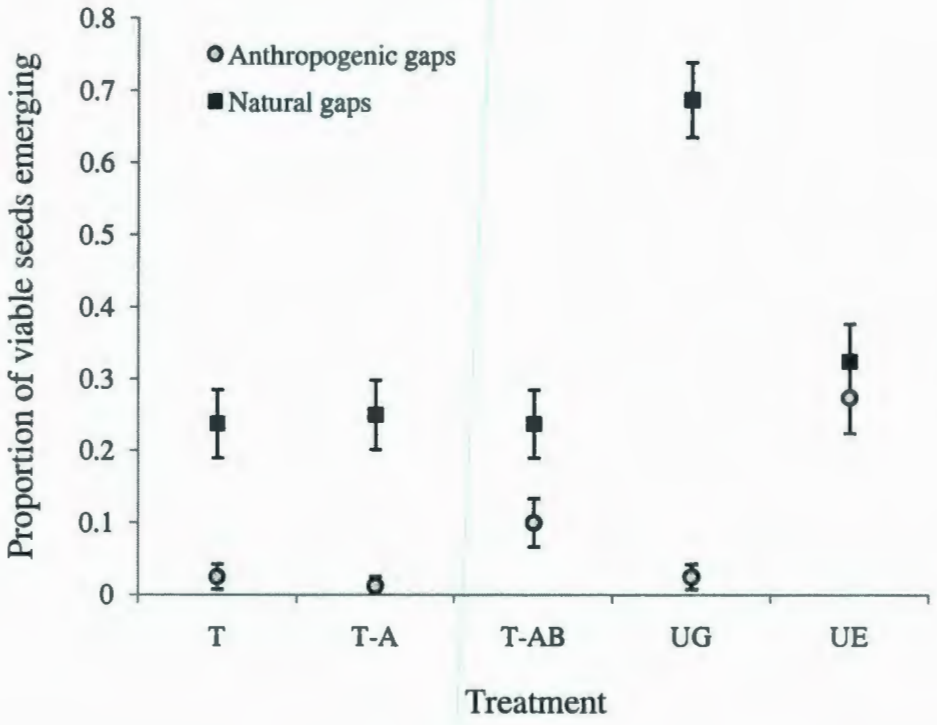

Figure 3.1 – Mean (± SE) proportion of viable balsam fir seeds emerging after planting seeds during July 2006 into five field treatments in boreal forest gaps within Gros Morne National Park disturbed by either anthropogenic or natural processes. Treatment abbreviations: T = Canada thistle monoculture, T_{-A} = thistle monoculture with aboveground shoot biomass removed, T_{-AB} = thistle monoculture with above- and below-ground biomass removed, UG = uninvaded region of the gap, and UE = uninvaded forest edge.

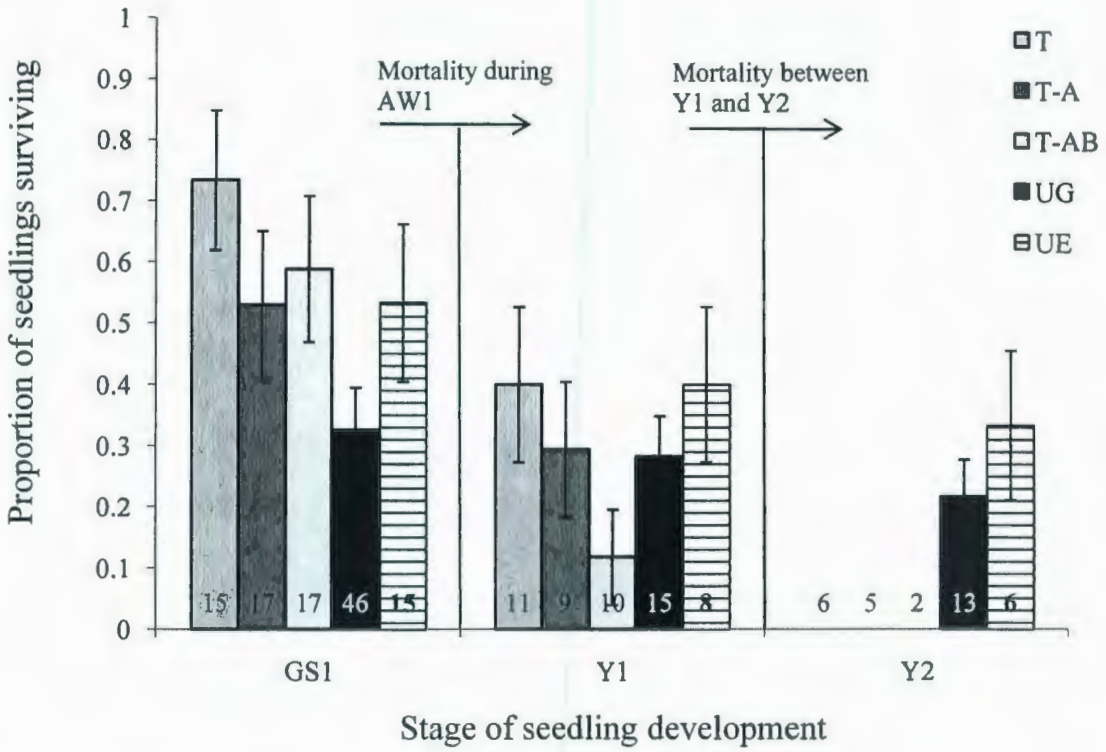

Figure 3.2 – Mean (±SE) proportion of newly emerged balsam fir seedlings surviving (after seeds were sown in July 2006) in five field treatments in **naturally disturbed** boreal forest gaps of Gros Morne National Park at the end of the first 2006 summer growing season (GS1), first year (June 2007; Y1), and second year (May 2008; Y2). AW1 = the first autumn-winter period. Sample sizes are indicated within bars and differ due to variable emergence and survival rates among treatments. Refer to Figure 3.1 for treatment abbreviations.

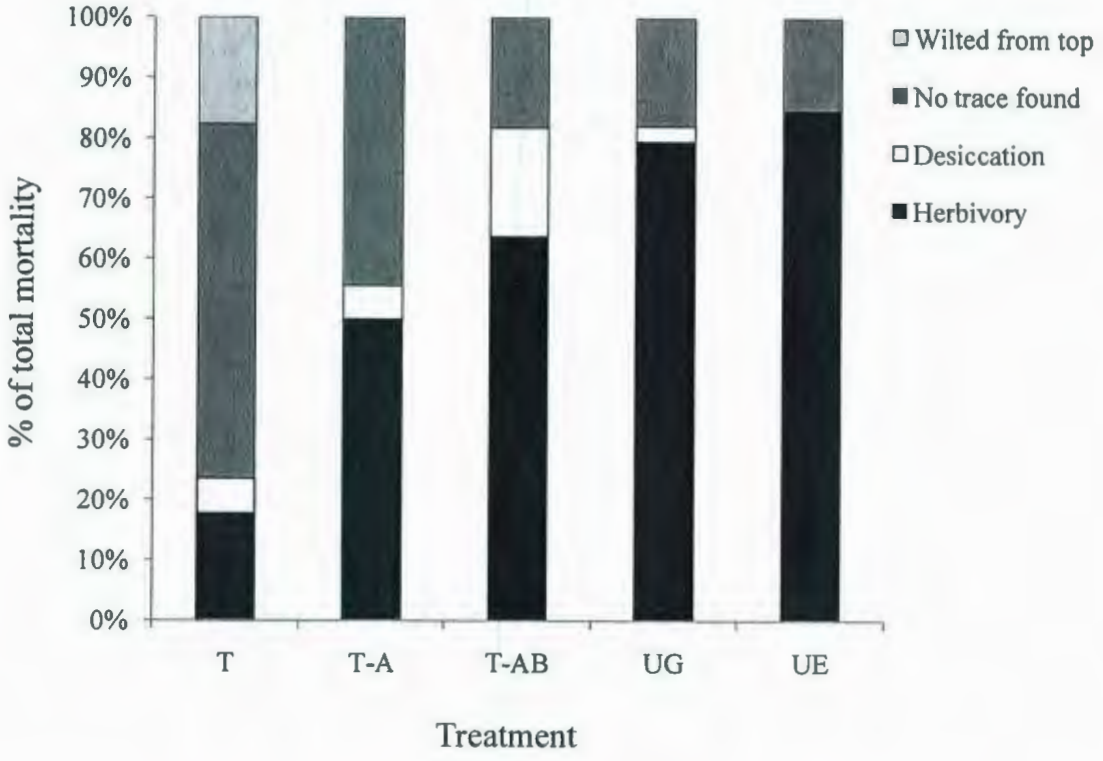

Figure 3.3 – Cause of mortality of balsam fir seedlings over the first two years of life after initial emergence in July 2006 in five field treatments in Gros Morne National Park, NL. Refer to Figure 3.1 for treatment abbreviations.

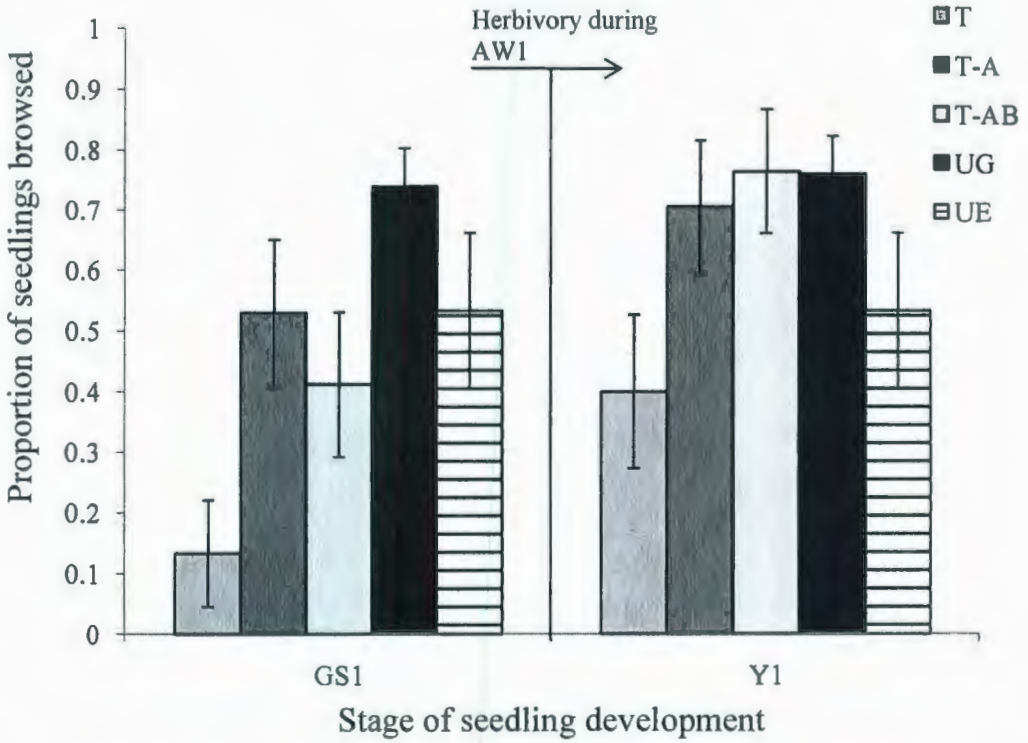

Figure 3.4 – Mean (±SE) proportion of newly emerged balsam fir seedlings having browse damage in five field treatments in **naturally disturbed** boreal forest gaps of Gros Morne National Park at the end of the first summer growing season (August 2006; GS1) and end of the first year (June 2007; Y1) after sowing seeds in July of 2006. AW1 = the first autumn-winter period. Refer to Figure 3.1 for treatment abbreviations.

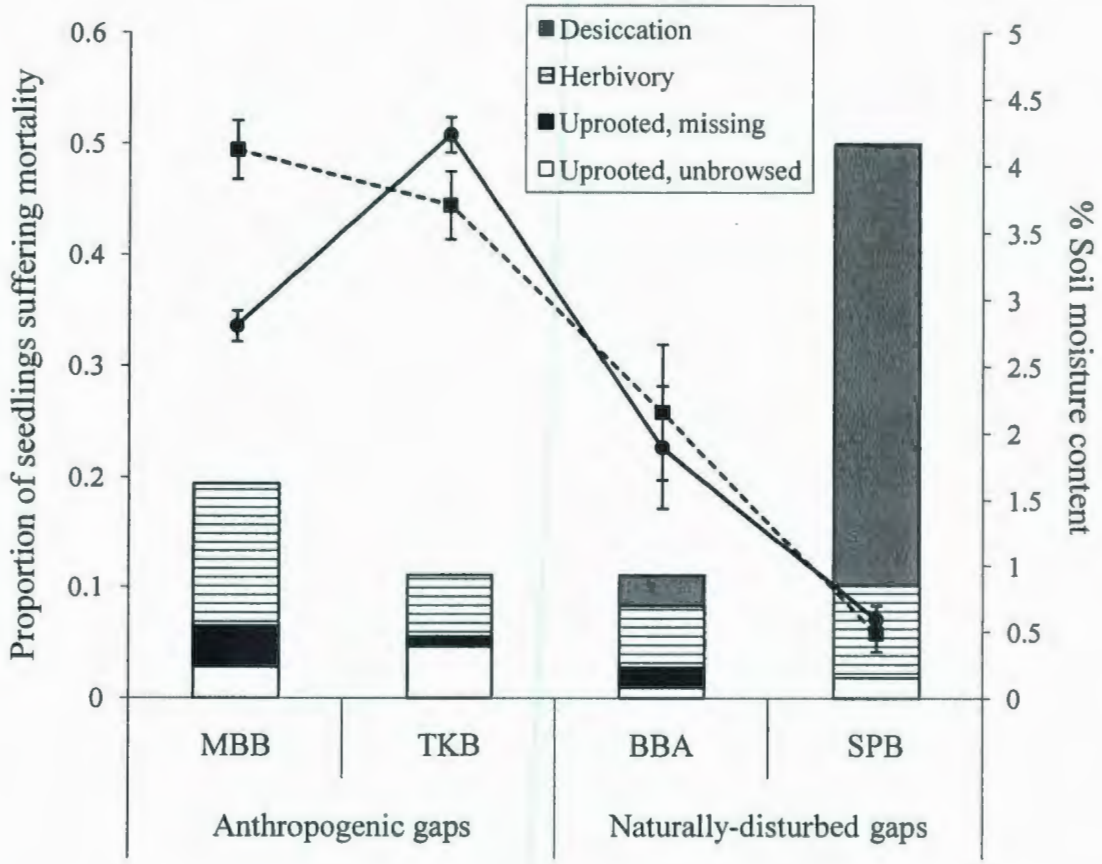

Figure 3.5 – Total proportion of balsam fir seedlings experiencing mortality, and the cause of this mortality, over the first year (Y1) after being transplanted at 15 months of age (in June 2007) into four boreal forest gaps in Gros Morne National Park disturbed either through anthropogenic or natural processes. Mean (± SE) percent soil moisture content for each gap as determined in the summer growing seasons in 2006 (the previous year; dashed line with square marker) and 2007 (year of planting; solid line with circle marker) are also indicated.

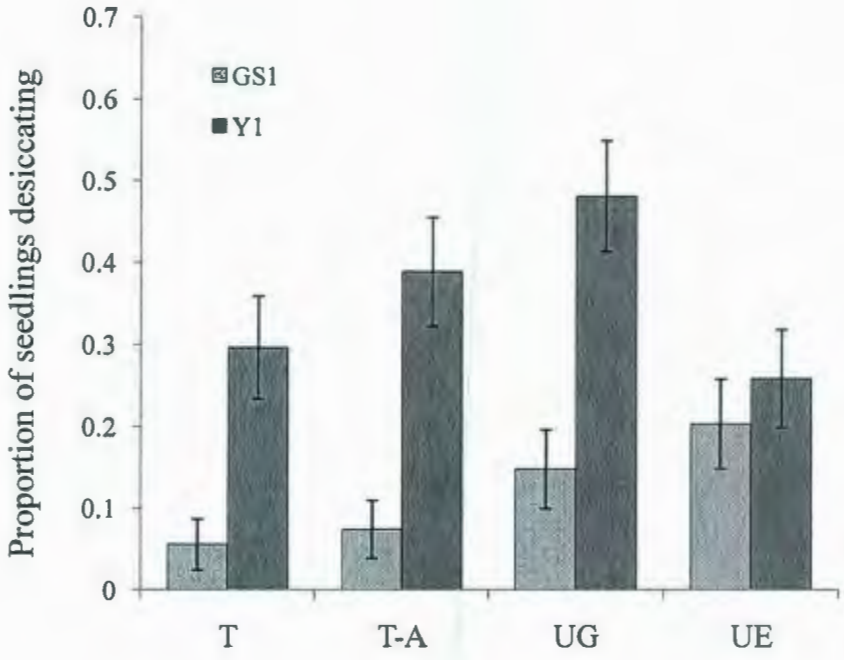

Figure 3.6 – Mean (±SE) proportion of balsam fir seedlings experiencing desiccation after 1) the first summer growing season (GS1), and 2) the first year (Y1) after being transplanted at 15 months of age (in June 2007) into four field treatments within **naturally-disturbed** boreal forest gaps in Gros Morne National Park. Refer to Figure 3.1 for treatment abbreviations.

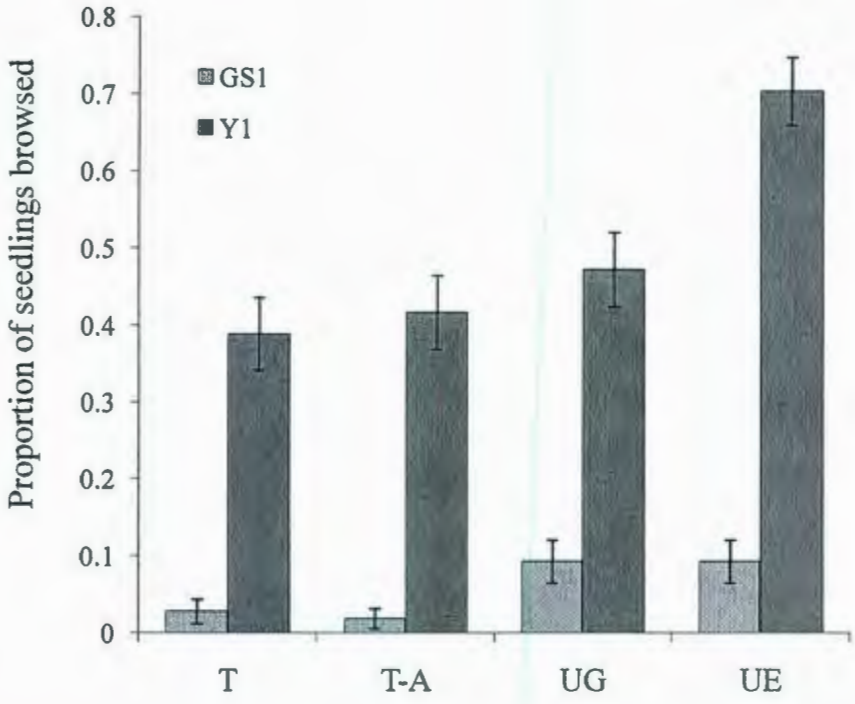

Figure 3.7 – Mean (±SE) proportion of balsam fir seedlings browsed after 1) the first summer growing season (GS1), and 2) the first year (Y1) after being transplanted at 15 months of age (in June 2007) into four field treatments within boreal forest gaps in Gros Morne National Park. Refer to Figure 3.1 for treatment abbreviations. Disturbance regimes are not distinguished as browsing patterns did not significantly differ among natural and anthropogenic gaps (Y1: treatment*disturbance ($F_{3,40}$=1.37, p=0.2652), disturbance ($F_{1,2.001}$ = 0.16, p=0.7266); GS1: stats not performed).

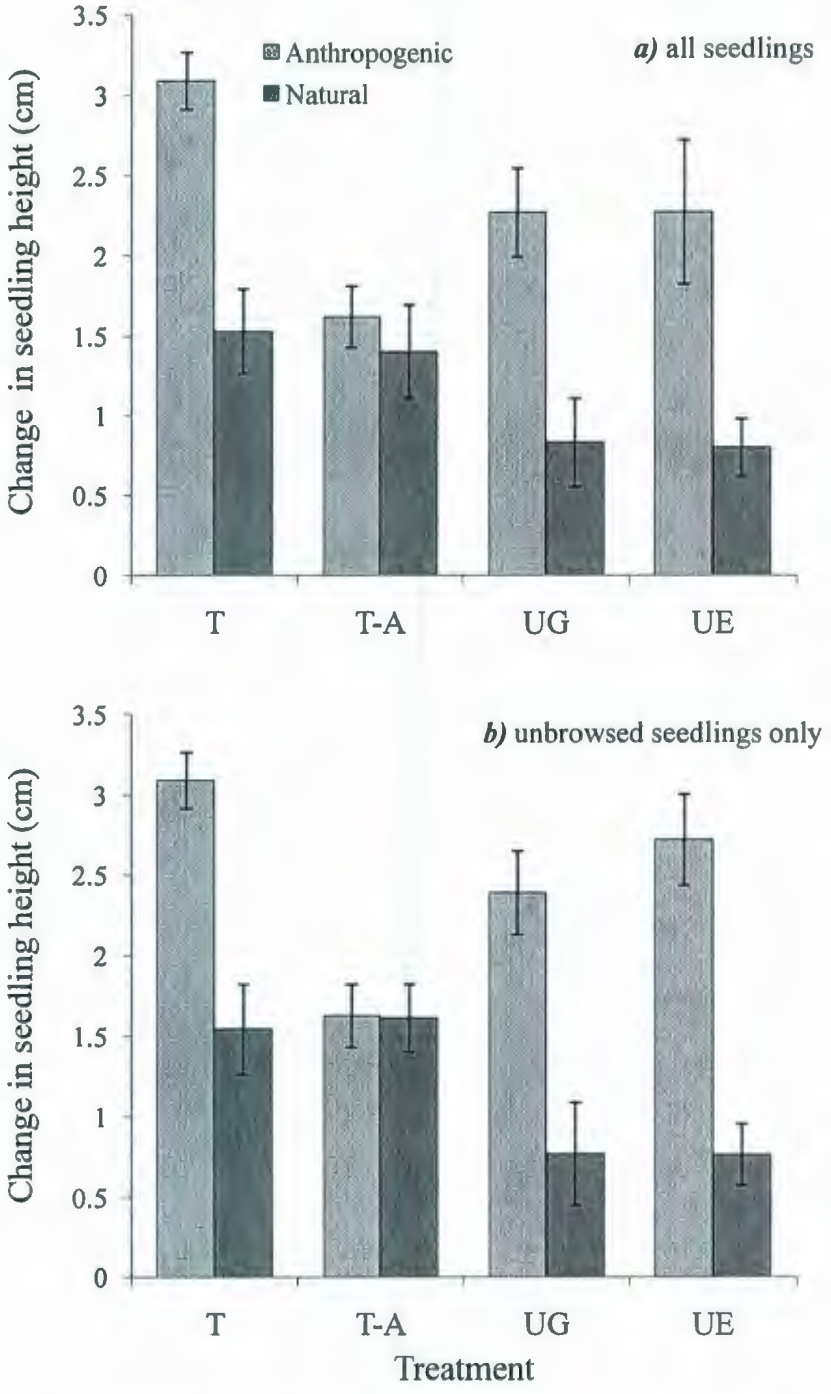

Figure 3.8 – Mean (±SE) change in balsam fir seedling height over the first summer growing season (GS1) after being transplanted at 15 months of age (in June 2007) into four field treatments within anthropogenically and naturally disturbed boreal forest gaps in Gros Morne National Park, NL. In *a)*, all seedlings have been included; in *b)* unbrowsed seedlings only are included. Refer to Figure 3.1 for treatment abbreviations.

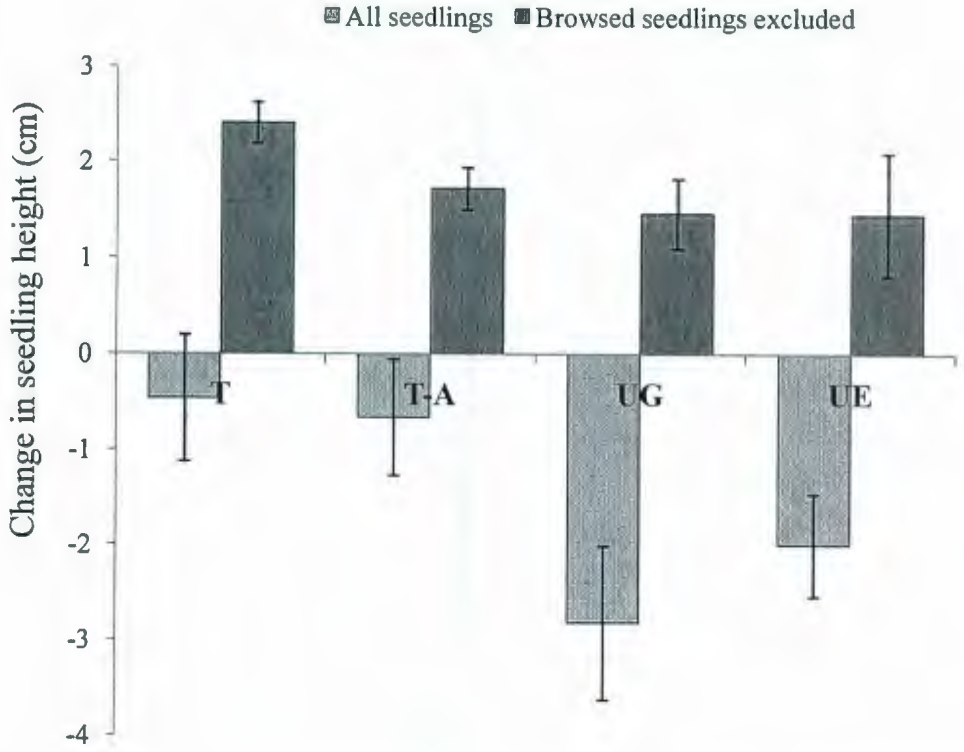

Figure 3.9 – Mean (±SE) change in balsam fir seedling height over the first year (Y1) after being transplanted at 15 months of age (in June 2007) into four field treatments within disturbed boreal forest gaps (disturbed either naturally or anthropogenically) in Gros Morne National Park, NL. Refer to Figure 3.1 for treatment abbreviations. Disturbance regimes are not distinguished as patterns in seedling height growth did not significantly differ among natural and anthropogenic gaps (see Table 3.4).

4. Inhibition of Boreal Tree Regeneration by an Invasive Non-Native Weed: The Potential Role of Allelopathy

4.1. INTRODUCTION

Non-native plant invasions can affect native species diversity, ecosystem structure and function, community dynamics, and successional pathways (Vitousek et al. 1997; Mack et al. 2000; Levine et al. 2003). However, the specific mechanisms by which invasive species impact native communities are often unclear (Levine et al. 2003; Orr et al. 2005). Allelopathy, the negative effect of one plant on another through the release of chemical compounds into the environment (Inderjit and Callaway 2003), is one mechanism by which some invasive, non-native plants become dominant in recipient communities, exclude native species, and often form monospecific stands (Ridenour and Callaway 2001; Hierro and Callaway 2003; Levine et al. 2003). Allelochemicals are products of secondary metabolism and may act directly on target plants by retarding growth, inhibiting germination through disruption of cell division, interfering with respiration and other energy-transfer processes, or inhibiting nutrient uptake or translocation (Fisher 1980). They may be released by volatilization (Glinwood et al. 2004), by leaching and exudation from the foliage, fruits, and roots (Fisher 1980), or by incorporation of litter into soil (Rice 1974, 1984). The many complex pathways of direct and indirect allelopathic interference between neighboring plants and its role in exotic plant invasions are only beginning to be elucidated (Inderjit 2001; Bais et al. 2003; Mangla et al. 2008).

Throughout North America, non-native Canada thistle (Asteraceae: *Cirsium arvense* (L.) Scop.) has a tendency to become highly invasive and to decrease native plant and animal species diversity (Stachon and Zimdahl 1980), to alter natural ecosystem structure (Nuzzo 1997; Zouhar 2001), and to contribute to the elimination of endangered and/or endemic plant species (Cheater 1992). Natural communities such as prairies, barrens, savannas, glades, sand dunes, fields and meadows that have undergone disturbance and/or are undergoing ecosystem restoration are particularly vulnerable to colonization by Canada thistle (Hutchison 1992; White et al. 1993). It is a major weed in agricultural landscapes where it can decrease crop yields and lead to significant monetary losses (Moore 1975; Kazinczi et al. 2001). The success of Canada thistle has been attributed, in part, to its high capacity for rapid clonal growth, reproduction, and range expansion (Moore 1975; Nadeau and Vanden Born 1989; Donald 1994; Heimann and Cussans 1996) as well as its superior competitive abilities (Robbins et al. 1970; Donald 1990). However, many studies have shown that allelopathy can also be an important mechanism of interference exerted by Canada thistle on neighboring vegetation (Bendall 1975; Stachon and Zimdahl 1980; Putnum 1984; Ghosh et al. 2000; Kazinczi et al. 2001; Glinwood et al. 2004).

De Candolle (1832) reported reduction of oat (*Avena sativa* L.) growth by Canada thistle roots and was the first to provide evidence of injury resulting from chemical compounds excreted from Canada thistle. Bendall (1975) noted that in southern Tasmania, the growth of annual thistles was restricted to areas not colonized by *C. arvense* and in subsequent laboratory and glasshouse studies, found that water and

alcohol extracts of Canada thistle roots inhibited the germination of its own seedlings (suggesting autotoxicity) as well as that of subterranean clover (*Trifolium subterraneum* L.). Aqueous extracts similarly inhibited growth of six of seven assayed species including its own seedlings and three native thistle species. After noting that the degree of inhibition of native vegetation by Canada thistle in the field was related to the age of the monoculture, Bendall (1975) suggested that allelochemicals from Canada thistle accumulate in soil and illustrated that inhibition of growth also occurred when the above species were grown in soil containing Canada thistle residue (Bendall 1975). Stachon and Zimdahl (1980) reported that ethanol extracts of Canada thistle roots and foliage reduced radicle growth of various crop species in petri dishes, but did not affect germination rates. When Canada thistle litter, roots, and foliage were then added to soil in a greenhouse bioassay, reductions in growth occurred in three of the four species assessed (Stachon and Zimdahl 1980). Similarly, in a series of greenhouse experiments, Wilson (1981) showed that Canada thistle residues and leaf leachates significantly reduced the growth of sugarbeet (*Beta vulgaris* L.), alfalfa (*Medicago sativa* L.), wheat (*Triticum aestivum* L.), and corn (*Zea mays* L.) crops, as well as growth of Canada thistle plants. Several polyacetylene compounds have been identified as the potential source of allelopathy in Canada thistle (Binder and French 1994; Jordon-Thaden and Louda 2003) and various phenolic compounds known to contribute to allelopathic activity in other species have also been identified in Canada thistle exudates (Zakharenko and Aref'eva 1998; see Kazinczi et al. 2001 and Jordon-Thaden and Louda 2003 for thorough discussions).

Almost all previous research, however, has examined the effect of Canada thistle allelopathy on crop species rather than on native plants in the recipient community (e.g. Stachon and Zimdahl 1980; Wilson 1981; Kovács et al. 1988). Also, many researchers have used extract bioassays (e.g. Bendall 1975; Kovács et al. 1988; Solymosi and Nagy 1999; Kazinczi et al. 2004), which may not reflect true interactions in the field, especially when soil is not used as a growth medium (Inderjit 2001). Thus, it is not clear whether allelopathy plays a role in Canada thistle's displacement of native plants in natural ecosystems.

In Gros Morne National Park (GMNP), Newfoundland (Canada), severe infestations of Canada thistle have recently been recorded throughout remote boreal forest canopy openings created by either natural processes (i.e. insect outbreaks) or anthropogenic disturbance (i.e. small-scale domestic timber harvesting). Surveys indicate that 41% of all harvested areas and 55% of naturally-disturbed gaps created within the past 30 years currently contain Canada thistle (Parks Canada, unpublished data), which frequently occurs as dense monocultures (i.e. up to 48 shoots/m^2; Chapter 2). It is highly unusual that this exotic plant has spread from along roadsides into small, remote, unconnected canopy gaps throughout otherwise continuous protected boreal forest, because Canada thistle is usually found in areas of high anthropogenic disturbance such as roadsides, ditches, waste places, agricultural fields, and abandoned pastures (FNA 2007). This exotic species has not generally been considered a threat to boreal forest areas due to its high light requirements (Haber 1997), but its dispersal and establishment in isolated forest gaps in GMNP appear to be facilitated by hyperabundant moose (*Alces*

alces L.) populations. These non-native herbivores act as conduits for the transport of alien plant propagules (via mud on their hooves and hair) into remote sites, and through browsing and trampling of native vegetation in gaps, which prolongs disturbance and prevents forest regeneration, create ideal conditions for alien plant establishment (Rose and Hermanutz 2004).

In GMNP, the emergence and early survival of balsam fir (*Abies balsamea* (L.) Mill.), the dominant native tree species in these boreal forests, is significantly lowered in areas with Canada thistle relative to uninvaded regions of forest gaps (Chapter 3). Physical removal of either aboveground Canada thistle biomass (i.e. by cutting shoots) or both above- and below-ground Canada thistle biomass (i.e. by digging up entire plants) do not improve emergence, suggesting that Canada thistle may pose a severe threat to stand regeneration through allelopathic or other indirect effects on soil which can remain after physical removal of the invader (Bendall 1975; Stowe 1979; Wilson 1981; Inderjit 2001). Allelopathy is often suggested as a causal mechanism behind the success of exotic invaders that form dense monotypic stands, as Canada thistle does, because this phenomenon is unusual in natural communities (Hierro and Callaway 2003; Levine et al. 2003).

It is important to better understand whether allelopathy is playing a role in Canada thistle's invasion of GMNP forests and prohibiting regeneration of native trees in canopy openings, as Park managers are currently evaluating potential methods of actively restoring non-regenerating gaps to a more natural forest. Knowledge of the existence of allelopathic effects of Canada thistle would aid the development of appropriate

management actions in thistle-invaded gaps. For example, if Canada thistle shoots or litter are found to inhibit native trees, a management strategy should not involve cutting or mowing of thistle shoots and leaving the decaying biomass on site. Allelopathic invaders present an additional challenge to reestablishment of native plant communities because the allelochemicals they produce may persist in the soil after the invaders themselves have been removed (Inderjit 2001). Additionally, if tree species are differentially inhibited, potential may exist for altered community composition (Orr et al. 2005) and successful management may require directed attention towards encouraging a particular native species.

In two greenhouse experiments, the effects of Canada thistle extracts and soil residues on the emergence, survival, and growth (in soil) of three dominant native tree species (balsam fir, white spruce (*Picea glauca* (Moench) Voss), and white birch (*Betula papyrifera* Marsh)) within GMNP and throughout eastern North American boreal forests (Bouchard et al. 1991) were examined. The native ranges of these North American tree species do not overlap with that of Canada thistle. In neither of these two experiments was our goal to identify specific allelopathic chemicals, nor was it to identify potential pathways of allelopathic action on native trees. As in Orr et al. (2005), the intent of this study was not to differentiate between direct effects of allelochemicals on target plants (Kobayashi 2004) and associated, indirect biotic and abiotic effects of allelochemicals (e.g. nutrient cycling, microbial activity) on the soil environment (Inderjit and Weston 2000; Inderjit and Weiner 2001). Instead, these experiments were designed to provide

information relevant for forest management and as a first step towards better understanding the dynamics between Canada thistle and native boreal forest trees.

In the first experiment, three questions were addressed: 1) Does Canada thistle inhibit native boreal forest tree species, and if so, which part of Canada thistle is responsible for the inhibition?; 2) If Canada thistle indeed inhibits native trees, which aspect of their life history (i.e. germination, growth, or survival) is most affected?; and 3) How do the three different native species differ in their response to Canada thistle? To answer these questions, realistic aqueous extracts from Canada thistle parts (e.g. shoots, roots, soil, and litter) were applied to native tree seeds planted in soil. It was hypothesized that both aboveground and belowground biomass from Canada thistle would severely inhibit the success of all native tree species tested.

The purpose of the second experiment was to help predict what the condition of the remaining soil in forest gaps may be for tree re-establishment after removal of Canada thistle. To achieve this, the allelopathic potential of soils that recently supported dense growth of Canada thistle was explored and the success of balsam fir, white birch, and white spruce in these soils was compared with similar soils that did not support thistle growth. Activated charcoal (AC) was used to help determine if allelopathic substances exist in soil that previously supported Canada thistle. Activated charcoal added to soil is expected to ameliorate any potential allelopathic effects because of its high affinity for adsorbing to organic compounds such as allelochemicals (Callaway and Aschehoug 2000). Although activated charcoal indiscriminately binds organics, this usually benefits native plants (Callaway and Aschehoug 2000; Ridenour and Callaway 2001; Kulmatiski

and Beard 2006) because native species are likely to have evolved resistance to allelochemicals from native plants in the same region but are much more likely to be naïve to allelochemicals released by exotic plants (Bais et al. 2003; Vivanco et al. 2004). It was hypothesized that native trees grown in soil collected from under Canada thistle monocultures would be less successful than those in uninvaded soil, and that addition of activated charcoal would minimize these effects and provide support for allelopathic impacts of Canada thistle. This experiment was conducted in soil collected from under Canada thistle monocultures in invaded forest canopy openings in GMNP, and repeated simultaneously in potting soil (a commonly utilized growth medium in allelopathy studies) in which Canada thistle had been grown, as a comparison against the more natural soil conditions. Additionally, because it is well known that allelopathic mechanisms are often manifested through alteration of beneficial microbial associations with the roots of neighboring native plants (Rice 1979; Ponder 1986) and changes in these microbial communities may impact the ability of native species to recolonize habitat after removal of the invader (Wolfe and Klironomos 2005; Smith et al. 2006), trial inoculations of mycorrhizal fungi were also performed on a subset of the native tree species in each treatment to determine if this potential management step would increase their success in the soil. Balsam fir, white spruce, and white birch are all known to form ectomycorrhizal (EM) associations, and white birch may also occasionally form vesicular-arbuscular mycorrhizal (VAM) associations (Malloch and Malloch 1981, 1982), therefore these species could be particularly susceptible to loss of mycorrhizae.

4.2. METHODS

Study area / Field collections

All field collections of thistle material (Experiment 1) and soil (Experiment 2) were harvested under permit in boreal forest canopy openings in Gros Morne National Park, located on the western coast of the island of Newfoundland, Canada (49.5°N, 57.9°W). GMNP is eastern Canada's second largest national park at 1805 km² and lowland forests comprise 43% of the park's total area (Rose and Hermanutz 2004). The coastal lowland forest region is characterized by cool summers (July mean: 15°C) and mild winters (February mean: -7.5°C) moderated by an oceanic influence, a short growing season of 140-150 days, strong prevailing southwesterly and westerly winds (Bouchard et al. 1991; Burzynski et al. 2005), and 1200-1450 mm of annual precipitation (Banfield and Jacobs 1998). Soils in the park are primarily humo-ferric podzols characterized by poorly drained acidic, mineral soils and formed under the influences of the parent material, humid climate, and coniferous vegetation (Clayton et al. 1977). All materials were collected from four forest gaps in the park and pooled (Note: these four gaps correspond to sites MBA, MBB, TKB, and BBA described in Table 3.1 in Chapter 3). These canopy openings were created by either natural (insect infestations; BBA) or anthropogenic (domestic harvesting; MBA, MBB, TKB) disturbance regimes between 1983 and 1997. The surrounding lowland forest was composed predominantly of balsam fir mixed with white spruce, white birch, and black spruce (*Picea mariana* (Mill.) B.S.P.). Elevations of the gaps ranged between 56 and 99 m above sea level and slopes faced southwest; gaps were separated by up to 17 km. Each gap was partially invaded by

Canada thistle monocultures; the diameter of these monocultures ranged from approximately 11 m to 32 m. Average Canada thistle shoot density in these monocultures ranged between 10 and 22 shoots/m^2 among gaps, with an overall mean Canada thistle density of 15 shoots/m^2 (Humber, unpublished data).

All collections of Canada thistle samples and field soil were performed during the first week of July in 2007. This corresponded to the time period of natural germination and early growth of the three tree species in GMNP. At the time of collection, Canada thistle shoot height was no more than 50 cm, although heights frequently reached >150 cm later in the summer before dying back for the winter.

Due to a low local seed crop during the year prior to the study, all native tree seeds were provided by the National Tree Seed Centre, Canadian Forest Service (Fredericton, NB). Balsam fir seeds were derived from Bay D'Espoir, NL, white spruce from Woody Point, NL, and white birch from Indian Brook, Nova Scotia, and had documented germination rates of 50.0%, 90.0%, and 90.0%, respectively. Attempts to confirm these documented germination rates using controlled germination tests in an environmental chamber were unsuccessful due to excessive mold growth within the petri dishes and lack of additional seeds to repeat the trials; yet, results of the allelopathy experiments revealed that balsam fir viability was in fact much greater than 50.0%. As per NTSC protocol, balsam fir and white spruce seeds were moist stratified at 4°C for three weeks prior to planting and prior to germination tests to break dormancy; white birch seed did not require pre-treatment. Experiments were performed in a greenhouse at

the Memorial University of Newfoundland's Botanical Garden in St. John's, Newfoundland (Canada).

Experiment 1: Aqueous extracts

To test the impact of Canada thistle on the emergence, growth and survival of three native boreal forest trees, thistle extracts were created from: 1) whole, fresh shoots (i.e. stems and leaves), 2) minced shoots, 3) whole, fresh roots, 4) decaying leaf litter on the soil surface, and 5) soil from the top 15 cm beneath living plants. As in Orr et al. (2005), a minced leaf extract treatment was included for comparison since this has historically been the method of preparing extracts in allelopathy bioassays (e.g. Bendall 1975; Kazinczi et al. 2004) but may exaggerate potential allelopathic effects and give results that are less ecologically realistic than extracts derived from whole shoots and roots (Inderjit and Callaway 2003). Two control treatments included: 6) deionized water and 7) an extract from whole balsam fir seedlings (<30 cm). The balsam fir extract was included as an additional control due to reports that it exhibits autotoxicity (Thibault et al. 1982; Singh et al. 1999). It was therefore of interest to include this extract to determine if our methods of extract preparation and experimental design would reveal this condition in balsam fir and, if so, to compare the strength of its autotoxic effect to any potential effects of the Canada thistle extracts.

Similar to Orr et al. (2005), realistic concentrations of the exotic plant extracts were created by calculating the surface area of a single-seedling pot and watering each seedling with a volume of extract representative of the quantity of rainfall that would pass

through the same surface area of Canada thistle in the field. The total surface area experienced by tree seeds/seedlings in each treatment was calculated (60 pots per treatment × 3 tree species × 8.55 cm^2 surface area per pot ~ 1540 cm^2 total surface area) and then, from the equivalent surface area in the field, Canada thistle foliage, roots, litter, and soil (to a 15 cm depth) were each collected for preparation of extracts. Whole balsam fir seedlings <30 cm in height (i.e. shoots and roots) were additionally collected from the same surface area in adjacent undisturbed forest. The total surface area of each extract (i.e. 1540 cm^2) was collected from the four invaded forest gaps described above, from four randomly-chosen subsamples per site, and pooled. The 10-year local rainfall average during the 10 week (July 10- September 17) duration of the experiment (Environment Canada 2009) was determined and multiplied by the total treatment surface area to determine a realistic volume for each extract (i.e. 23.5 cm rainfall × 1540 cm^3 ~ 36.2 L per treatment). Whole plant parts or soil were soaked in 36.3 L of deionized water for 24 hours at room temperature and strained through three layers of cheesecloth to remove particulates. The minced shoots treatment was prepared as above but by first chopping to <3mm in a food processer. In an effort to replicate conditions as similar as possible to those that may occur in the field, extracts were not fine filtered (which would have been difficult as a result of the quantity of extract) or sterilized. Therefore, direct impacts of allelochemicals and indirect effects of associated microbes can not be distinguished here (Orr et al. 2005). To help limit microbial growth, extracts were stored in closed dark-tinted glass containers in a cold room at 4°C for the duration of the experiment.

On 10 July 2007, seeds were planted in 3.3 cm diameter pots containing 55 mL of field-derived soil that was collected to 15 cm depth from the adjacent undisturbed forest edges of the four GMNP gaps described above. Soil samples were pooled and mixed thoroughly. One seed was planted per pot and seeds were assigned randomly to the extract treatments. Each of the seven treatments was replicated in 60 pots per tree species for a total of 180 pots per treatment; 1260 pots in total. Pots were randomly distributed within the greenhouse and their position rotated every three days. Natural light/darkness cycles were maintained in the greenhouse as a result of its transparent roof. The pots were watered with the assigned extract immediately after planting and at three day intervals for the entirety of the experiment. Each pot received a total of 201 mL of extract over the 10 week experimental period (36.2 L / 180 pots ~ 201 mL) by watering with 8.8 mL of extract every third day (201 mL / 23 watering days ~ 8.8 mL) using a syringe.

Seedling emergence and survival was monitored at three day intervals. Only seedlings that penetrated the soil surface were considered to be successfully emerged. At the end of the 10 week period, all seedlings were harvested and their shoot length measured with calipers to the nearest 0.001 cm. A subset (n=20) of seedlings from each treatment were severed at the root collar, separated into aboveground and belowground parts, carefully rinsed to remove all soil, and dried in a 70°C oven for 48 hours. Aboveground and belowground dry biomass was determined to the nearest 0.0001 g using an analytical balance.

Experiment 2: Residues in soil

To determine the suitability of field soils previously supporting Canada thistle monocultures for sustaining native tree species, and to investigate if allelopathic residues may remain in these soils, four soil treatments were used as growth mediums:

1) *Field soil previously supporting a C. arvense monoculture (+C.a.)* – in early July of 2007, field soil was removed to 15 cm depth underneath Canada thistle monocultures growing in four boreal canopy openings in GMNP (see previous description of the four sites), transported from the field, and transferred into pots in the greenhouse after being pooled and thoroughly mixed.

2) *Field soil previously supporting a C. arvense monoculture, with activated charcoal added (+C.a.$_{AC}$)* – as treatment 1, with powdered extra-pure pro-analysis activated charcoal (Sigma-Aldrich Product #18001, Reidel-de Haën) added to the soil at a rate of 25 mL / 1 L of soil (2.5%).

3) *Field soil not invaded by C. arvense (–C.a.)* – soil was obtained from the same forest gaps as above, but from regions not invaded by Canada thistle and at least 15 m from the closest invaded area. For consistency, this soil was always collected from underneath the common, native boreal forest plant *Cornus canadensis* L. (i.e. bunchberry or crackerberry) which is commonly associated with all three native tree species.

4) Field soil not invaded by C. arvense, with activated charcoal added ($-C.a._{AC}$) – as treatment 3, with activated charcoal added. This was a control to test for the effect of activated charcoal in the absence of potential Canada thistle allelochemicals.

Although the experiment using field-derived soil described above was the main focus of Experiment 2, the above experiment was also simultaneously performed in potting soil, a commonly used growth medium in allelopathy studies, as a comparison against natural field soil conditions. This allowed the comparison of treatment effects among both soil types. For the equivalent *+C.a.* soil (treatment 1), in mid-October 2006 over 200 roots of Canada thistle were harvested from 10 invaded boreal forest gaps throughout GMNP (see Figure 3.1 in Chapter 3 for site descriptions). Roots were transferred into wooden flats containing soil from the field and left to overwinter outside. Shoot emergence from the flats in early May of 2007 corresponded with the natural period of Canada thistle emergence in the field. At this time, Canada thistle plants were transplanted to large pots containing potting mix (CIL Smart Mix 0.03-0.03-0.03, Nu-gro IP Inc., Brantford, Ontario) at a density of 15 shoots/m^2 to mimic the average shoot density in GMNP monocultures. Pots remained outside of the greenhouse until early July 2008 during the period of field soil harvesting in GMNP. At this time, each entire thistle plant was removed from the potting soil which was then thoroughly mixed and transferred into individual pots within the greenhouse. The *–C.a.* treatment in potting soil was potting mix that received the same handling as in treatment 1 but was not planted

with Canada thistle. Treatments 2 (+$C.a._{AC}$) and 4 (–$C.a._{AC}$) involved the addition of activated charcoal as above.

Seeds of the three native tree species (balsam fir, white spruce, white birch) were planted on 10 July 2007 and randomly assigned to treatments. One seed was planted per 3.3 cm diameter pot containing 55 mL of the assigned soil treatment. Sixty replicate pots were planted for each treatment for a total of 1440 pots (4 treatments × 2 soil sources × 3 species × 60 replicates = 1440). In addition, one half (n=30) of each soil treatment received a mycorrhizal fungi inoculation (MYKE Pro AN1, Premier Tech Ltd, Rivière-du-Loup, Quebec) containing assemblages of both ectomycorrhizae and vesicular-arbuscular mycorrhizae immediately prior to planting. The granular inoculant was added at 10% of the soil volume (i.e. 5.5 mL per pot) and mixed thoroughly throughout. Pots were randomly distributed within the greenhouse and their position rotated every three days. Each pot was watered with tap water immediately after planting and at three day intervals for the duration of the experiment.

Seedling emergence and survival was monitored at three day intervals. At the end of the 10 week period, seedlings were harvested and their shoot length, aboveground- and belowground- biomass determined as in experiment 1.

Statistical analyses

All statistical analyses were performed on SAS version 9.1 (SAS Institute, Cary, NC, USA). In experiments 1 and 2, where the response variable consisted of binary or proportional data (i.e. proportion of seedlings emerging, proportion of seedlings

surviving to end of 10 week period), logistic regression, a special case of the Generalized Linear Model used for analyzing binary or proportional response data with continuous, categorical, or both types of explanatory variables (Agresti 1996), was used (Proc GENMOD, SAS Institute, Cary, NC, USA). Logistic regression is the most appropriate and flexible test for the above data as it addresses the binomial distribution of the residuals by applying a logit transformation (Trexler and Travis 1993; Agresti 1996; Lewis 2004). Where the response variable was a count (i.e. number of days to emergence; number of days surviving), a generalized linear model with a Poisson distribution and log link was applied (Proc GENMOD, SAS Institute, Cary, NC, USA). All test assumptions were satisfied as determined through examination of residuals and model fit statistics. If a model was slightly overdispersed, a Pearson scale correction factor was applied (Littell et al. 2002). For the analysis of shoot length, where the response variable was a continuous regression variable, an analysis of variance (ANOVA) was performed (Proc GLM, SAS Institute, Cary, NC, USA). Aboveground and belowground biomass estimates taken on a subset of surviving seedlings (n=20) were combined into a MANOVA (Proc GLM, SAS Institute, Cary, NC, USA). When effects were significant in the multivariate analysis, univariate F-tests were examined for each individual response variable. All test assumptions for the analyses of variance were met as determined through examination of residuals for normality, homogeneity, and independence. Significant differences were accepted at $\alpha < 0.05$.

Experiment 1

Fixed effects in experiment 1 included: treatment (with seven levels), tree species (with three levels), and the treatment × species interaction. When the effect of treatment was significant, linear contrasts were used to compare each treatment to the deionized water control. An additional contrast compared the fresh whole shoots treatment to the minced shoot treatment. Contrast α-values were Bonferroni corrected for seven comparisons ($\alpha' = 0.00714$). Results of multiple comparisons were deemed marginally statistically significant when $0.00714 < p < 0.05$. Where the interaction between treatment and species was significant, the effect of treatment was determined separately for each tree species.

Experiment 2

Fixed effects in experiment 2 included tree species (with three levels), treatment (with four levels: +*C.a.*, +*C.a.*$_{AC}$, –*C.a.*, and –*C.a.*$_{AC}$), mycorrhizae (with two levels: present or absent), and soil type (with two levels: field soil or potting soil). All possible interactions were included in a full factorial arrangement. Due to numerous 2- and 3-way interactions of species with other variables in all analyses, each tree species was analyzed separately in all analyses except for shoot length, where no interactions occurred. When interactions between soil type and other variables indicated differential patterns in treatment (e.g. soil type*treatment) and/or mycorrhizae (e.g. soil type*mycorr) effects in field soil as opposed to potting soil, analyses were performed separately for each soil type.

When the effect of treatment was significant, linear contrasts were performed to test three specific *a priori* hypotheses (Table 4.1). Contrast α-values were Bonferroni corrected for three comparisons ($\alpha' = 0.0167$). Results of multiple comparisons were deemed marginally statistically significant when $0.0167 < p < 0.05$.

4.3. RESULTS

Experiment 1

Emergence

In total, 788 of the 1260 sown seeds emerged over the duration of the experiment. Overall emergence of white birch, balsam fir, and white spruce averaged among all treatments was 48.6%, 69.0%, and 70.0%, respectively. Seedling emergence began approximately nine days after planting and no new emergence was recorded after day 39. Response of seedling emergence to the Canada thistle extracts differed among the three native tree species (treatment × species $\chi^2 = 22.38$, df = 12, $p = 0.0335$). Although white birch emergence was 16.7% lower in the minced extract than the control, there was no significant difference among the treatments ($p = 0.1178$; Figure 4.1*a*). Similarly, balsam fir emergence did not differ among extract treatments ($p = 0.9995$; Figure 4.1*b*). Emergence of white spruce differed significantly among the extract treatments ($p = 0.0392$; Figure 4.1*c*), but contrasts revealed that none of the extract treatments had significantly different levels of emergence than the deionized water control, despite the minced and root extract treatments having over 10% higher emergence than the control. The percentage of white spruce seedlings emerging in the minced shoot treatment (mean

± SE: 78.3% ± 5.3%) was 1.34 times higher than in the whole shoot treatment (58.3% ± 6.4%) but this contrast was only marginally significant after Bonferroni correction ($p = 0.0178$).

The effect of the Canada thistle extracts on time to seedling emergence varied among tree species (treatment × species $\chi^2 = 76.64$, $df = 12$, $p < 0.0001$). In all three trees, time to emergence significantly differed among treatments (Figure 4.2*a-c*). In white birch, the whole shoot extract decreased the mean number of days to emergence by 25% (i.e. 4.2 days), relative to the control ($p < 0.0001$; Figure 4.2*a*) and the balsam fir extract decreased the mean time to emergence by 18%, or 3.0 days ($p = 0.0025$; Figure 4.2*a*). The mean time to birch emergence was significantly faster (i.e. by 5.5 days) in the whole shoot extract than in minced shoots ($p < 0.0001$; Figure 4.2*a*). For balsam fir, days to emergence was significantly decreased by the soil extract alone by an average of 2.7 days ($p = 0.0015$; Figure 4.2*b*). In contrast, days to emergence in white spruce did not significantly differ from the water control for either of the extracts despite an overall significant difference between all treatments (Figure 4.2*c*).

Survival

White birch was excluded from the analysis of survival as well as from analyses on seedling growth (i.e. shoot length and biomass) due to the occurrence of browsing on foliage within the greenhouse by an unknown insect approximately seven weeks after initiation of the experiment. Birch was not excluded from the two preceding analyses (i.e. emergence, days to emergence) because all seedling emergence had been completed prior

to this time period. Therefore the main model examined survival, which was conditional upon initial emergence, in balsam fir and white spruce only. Overall, 69.7% (118/204) of balsam fir seedlings and 86.7% (255/294) of white spruce seedlings survived over the 10 week experimental period. Seedling survival of the two native tree species diverged in response to the Canada thistle extracts (treatment × species $\chi^2 = 18.06$, df = 6, p = 0.0061). In both species, survival was significantly influenced by extract identity (balsam fir: p = 0.0003; white spruce: p = 0.0032; Figure 4.3*a-b*). In balsam fir, three of the treatments exhibited lower survival rates than in the water control (Figure 4.3*a*). The largest decrease in fir survival rates was seen in the seedlings receiving the balsam fir extract, however this 26.9% reduction in survival was only marginally significant after Bonferroni correction (p = 0.0126). Balsam fir survival was significantly (27.6%) lower in the whole shoots extract than in the minced shoots (p = 0.0051). In white spruce, the whole shoot extract significantly decreased seedling survival by 29.0% (p = 0.0003; Figure 4.3*b*). Survival was also lowered in minced shoot and litter extracts relative to the control, although these differences were only marginally significant after Bonferroni correction (p = 0.0081 and p = 0.0243, respectively; Figure 4.3*b*).

Growth

The response of balsam fir shoot length to the extracts differed from the response of white spruce (treatment × species $F_{6,444} = 4.24$, p = 0.0004). The shoot lengths of each species was significantly different among extract treatments (balsam fir: p = 0.0263; white spruce: p = 0.0075; Figure 4.4*a-b*). However, comparisons of shoot lengths in each

extract treatment to the deionized water control indicated no statistically significant reductions for either fir or spruce after Bonferroni correction. Rather, there was a marginal increase in height relative to the water control for fir seedlings receiving the whole shoot ($p = 0.0158$) and minced shoot ($p = 0.0210$) extracts (Figure 4.4*a*) and for spruce seedlings receiving the root extract ($p = 0.0147$; Figure 4.4*b*).

Analysis of seedling biomass using MANOVA revealed that both balsam fir and white spruce seedling biomass exhibited strong but differing responses to the extracts (Table 4.2). There was a strong correlation between aboveground and belowground biomass in both balsam fir (88.5% correlation) and white spruce (73.4%) seedlings. In balsam fir, the extract treatments primarily affected aboveground seedling biomass (Table 4.2) such that the whole shoot and minced shoot extracts significantly increased aboveground biomass relative to the deionized water control by 46.5% ($p = 0.0003$) and 48.3% ($p = 0.0023$), respectively (Figure 4.5*a*). Fir seedlings receiving the litter extract also had 1.31 times more aboveground biomass than the control, although this increase was only marginally significant after Bonferroni correction ($p = 0.0309$). In white spruce, both aboveground and belowground biomass was significantly affected by the extract treatments (Table 4.2). The fir extract significantly increased aboveground ($p = 0.0005$) and belowground ($p = 0.0095$) spruce biomass relative to the control by 62.2% and 45.2%, respectively (Figure 4.5*b*). Aboveground spruce biomass was also marginally increased by the root ($p = 0.0452$) and soil ($p = 0.0500$) extracts and belowground biomass was marginally increased by the soil extract ($p = 0.0383$; Figure 4.5*b*).

Experiment 2

Emergence

Overall levels of emergence were high, with 71.3% (1027/1440) of the sown seeds emerging over the experimental period. Seedling emergence began approximately eight days after planting and no new emergence was recorded after day 30. Overall emergence for white birch, balsam fir, and white spruce was 58.8%, 77.9%, and 77.3%, respectively. Due to differential responses of white birch to treatments within the two soil types (treatment*soil type; Table 4.3), the effects of treatment and mycorrhizal inoculation on birch emergence were examined separately for field-derived and potting soil. This was not necessary for balsam fir or white spruce, as both soils performed similarly (Table 4.3). To simplify and focus the results, in all instances where soil types were examined separately due to significant interaction terms, only those results in field-derived soil are presented (results in potting soil can be found in Appendix III) as these results are expected to more closely reflect actual processes and patterns of allelochemical impact occurring in nature (Inderjit and Dakshini 1995; Inderjit 2001). There was a significant effect of treatment on birch emergence in field-derived soil ($p<0.0001$; Figure 4.6*a*). Birch emergence did not differ between Canada thistle-derived field soils and non-thistle soil (Contrast 1, Table 4.1: *+C.a.* vs. *–C.a.*; $p = 0.8262$). However, addition of activated charcoal to each resulted in significantly different emergence patterns, cutting germination in half in non-thistle soils (Contrast 3: *–C.a.* vs. $–C.a._{AC}$, $p < 0.0001$) but increasing emergence 1.5 times in soils previously supporting thistle (Contrast 2: *+C.a.* vs. $+C.a._{AC}$, $p = 0.0010$; Figure 4.6*a*).

In balsam fir, emergence differed significantly among treatments (Table 4.3). Fir emergence in +*C.a.* soil was 13.3% higher than in –*C.a.* soil ($p = 0.0101$; Figure 4.6*b*). Addition of activated charcoal to +*C.a.* soil lowered emergence by 10.8%, although the decrease was only marginally significant after Bonferroni correction ($p = 0.0336$; Figure 4.6*b*). In contrast, addition of activated charcoal to –*C.a.* soil (a control for the effect of activated charcoal in the absence of *C. arvense*; see Table 4.1) did not significantly change emergence ($p = 0.6564$; Figure 4.6*b*). White spruce emergence did not differ significantly among treatments (Table 4.3; Figure 4.6*c*).

In both white birch and white spruce, mycorrhizal inoculations significantly decreased emergence. Mycorrhizal effects were analyzed on white birch emergence in field soil only because of significant interaction terms (Table 4.3). White birch emergence in pots planted with field soil and receiving mycorrhizal additions was only 26% of the level of emergence in those not inoculated ($\chi^2 = 6.73$, $df = 1$, $p = 0.0095$; Figure 4.7). White spruce emergence in inoculated pots was also significantly decreased (by 11.7%) relative to the control ($\chi^2 = 6.15$, $df = 1$, $p = 0.0131$; Figure 4.7). Conversely, mycorrhizal additions had no effect on balsam fir emergence ($\chi^2 = 0.00$, $df = 1$, $p = 0.9923$; Figure 4.7).

There were significant interaction terms between soil type and treatment (Table 4.3) in the analysis of time to emergence for each of the tree species, due to different patterns of emergence among treatments in field soil vs. potting soil. The time to birch and balsam fir emergence in field soil did not differ significantly among treatments (white birch: $p = 0.0968$; balsam fir: $p = 0.2457$; Figure 4.8*a-b*) but did differ for white

spruce planted in field soil ($p = 0.0047$; Figure 4.8*c*). White spruce emergence occurred an average of 2.1 days earlier in +*C.a.* soil than in –*C.a.* soil ($p = 0.0162$). While the addition of activated charcoal to +*C.a.* soil did not significantly change the time to emergence (+*C.a.* vs. $+C.a._{AC}$; $p = 0.3317$), it significantly increased the time to emergence by 2.4 days in –*C.a.* soil (–*C.a.* vs. $-C.a._{AC}$; $p = 0.0061$; Figure 4.8*c*).

The effect of mycorrhizal fungi inoculation on days to emergence was examined only within field soil for white birch (due to significant treatment*mycorr*soil type interaction; Table 4.3), and it did not affect the time to emergence (field soil: $\chi^2 = 0.04$, df = 1, $p = 0.8474$). Similarly, inoculations did not impact the time to emergence for balsam fir or white spruce (Table 4.3).

Survival

As in experiment 1, white birch was excluded from the analysis of survival as well as from analyses of seedling growth (shoot length and biomass) due to defoliation by an unknown insect seven weeks after beginning the greenhouse experiment. Overall, 86.4% (323/374) of balsam fir seedlings and 86.0% (319/371) of white spruce seedlings survived over the 10 week experimental period. The effect of treatment on balsam fir seedling survival differed among the two soil types (i.e. significant treatment*soil type interaction; Table 4.3). Balsam fir survival in field soil differed significantly among treatments ($p = 0.0002$; Figure 4.9*a*). Survival of fir seedlings in thistle-derived field soil (+*C.a.*) was 12.9% less than in non-thistle (–*C.a.*) soil (Figure 4.9*a*). The addition of activated charcoal to thistle-derived field soil further decreased survival by 20.1% (Figure

4.9*a*). These differences were only marginally significant after Bonferroni correction ($p = 0.0424$ and $p = 0.0312$, respectively). Adding activated charcoal to *–C.a.* field soil had no effect on survival ($p = 0.4550$).

The proportion of white spruce seedlings surviving in potting soil was significantly higher than in field soil (Potting soil: 0.995 ± 0.002; Field soil: 0.800 ± 0.031; $\chi^2 = 14.99$, $df = 1$, $p = 0.0001$), but patterns of spruce survival among treatments were similar in each soil type (i.e. there were no interactions with the 'soil type' variable, Table 4.3). Spruce survival differed significantly among treatments ($p = 0.0335$; Figure 4.9*b*). The survival rate in *+C.a.* soil was 13.4% lower than in *–C.a.* soil; this difference was marginally significant after Bonferroni correction ($p = 0.0336$; Figure 4.9*b*). Although addition of activated charcoal to *+C.a.* soil did not change the survival rate (*+C.a.* vs. $+C.a._{AC}$; $p = 0.9352$, Figure 4.9*b*), its addition to the *–C.a.* control soil decreased spruce survival by 18.6% (*–C.a.* vs. $-C.a._{AC}$; $p = 0.0035$, Figure 4.9*b*).

Mycorrhizal inoculation did not impact the survival of balsam fir or white spruce seedlings (Table 4.3).

Growth

As above, white birch was excluded from analyses on seedling growth due to browsing damage. The lack of interaction between species and any of the variables in the full factorial model (i.e. treatment, mycorr, soil type, and their interactions) made it unnecessary to perform separate analyses of shoot length on each tree species. Seedling shoot length did not differ among treatments ($F_{3,609} = 0.46$, $p = 0.7088$), mycorrhizal

inoculation ($F_{1,609} = 0.12$, $p = 0.7286$), or soil type ($F_{1,609} = 0.46$, $p = 0.4962$). Shoot length differed significantly only between the two tree species (balsam fir: 2.83 cm ± 0.02 cm; white spruce: 2.14 cm ± 0.02 cm; $F_{1,609} = 410.5$, $p < 0.0001$).

A MANOVA analysis of seedling biomass indicated that treatment had no effect on balsam fir seedling biomass ($p = 0.3395$, Table 4.4). Balsam fir biomass varied significantly only between soil types ($p < 0.0001$; Table 4.4), with aboveground fir biomass 25.5% higher in field soil than in potting soil (field soil: 0.01814 g ± 0.00066 g; potting soil: 0.01445 g ± 0.00050 g; $p < 0.0001$) and belowground biomass 28.1% higher in field soil (field soil: 0.00802 g ± 0.00033 g; potting soil: 0.00626 g ± 0.00028 g; $p < 0.0001$). There was a 79.1% correlation between balsam fir aboveground and belowground biomass. Mycorrhizal inoculation had no effect on balsam fir biomass (Table 4.4).

Many interactions occurred between soil type and other variables in both the MANOVA and subsequent univariate ANOVAs for white spruce biomass (Table 4.4), indicating that spruce biomass differed greatly in its response to treatment and mycorrhizal inoculation depending upon the soil type in which it was planted. Aboveground or belowground biomass did not significantly differ among treatments in field soil (aboveground: $p = 0.2854$; belowground: $p = 0.0907$) despite a 19.4% higher aboveground biomass and 28.5% higher belowground biomass in *–C.a.* soil as compared to *+C.a.* soil (Figure 4.10). Effects of activated charcoal addition to *+C.a.* and *–C.a.* soil were minor (Figure 4.10). Mycorrhizae addition did not affect spruce aboveground biomass (treatment*mycorr: $F_{3,71} = 0.97$, $p = 0.4119$; mycorr: $F_{1,71} = 1.50$, $p = 0.2252$) or

belowground biomass (treatment*mycorr: $F_{3,71} = 2.48$, $p = 0.0677$; mycorr: $F_{1,71} = 2.20$, $p = 0.1622$) in field soil.

4.4. DISCUSSION

The results of both greenhouse experiments reveal that while Canada thistle exudates and residues in soil have little or no negative effects on emergence or growth of native trees, both have negative effects on early seedling survival of balsam fir and white spruce. The survival of each tree species was differentially impacted depending on the source of potential allelochemicals.

Experiment 1: Extracts

Realistic concentrations of aqueous Canada thistle extracts do not negatively affect the emergence of balsam fir, white spruce, or white birch. Various concentrations of the extracts were not tested to establish a dose response (Inderjit and Weston 2000) as the goal was to create concentrations of extracts that could exist under natural field conditions. Relatively few other studies have investigated the effects of allelopathic interference under ecologically relevant circumstances by using realistic sources and concentrations of allelochemicals (Inderjit and Weston 2000; Inderjit and Callaway 2003; Orr et al. 2005). Of all the extracts tested on the three tree species, only the Canada thistle minced shoots treatment was found to significantly decrease emergence of any species (i.e. white birch; 17% decrease). Unlike the other more realistic extracts tested, these finely minced shoots, although commonly-used in allelopathy bioassays, are not

considered to accurately reflect conditions occurring in nature (Inderjit and Callaway 2003; Orr et al. 2005). None of the extracts had any impact on emergence in balsam fir, whereas two of the extracts (i.e. minced shoots, roots) actually caused a slight (insignificant) positive effect on the proportion of white spruce emerging. Extracts also, under certain conditions, decreased the time to emergence of seeds. This was most evident for seeds of white birch, where whole Canada thistle shoot extracts decreased time to emergence (relative to the water control) by a mean of 4.2 days, and for balsam fir, where seeds receiving the soil extract emerged 2.7 days earlier on average.

These unexpected patterns of emergence likely resulted from the release of various compounds from the plant material used for extract preparation. As noted by Orr et al. (2005), stimulation of emergence rates by extracts may result from an array of factors including release of nutrients from decomposing plant tissue (Nilsen et al. 1999; Simons and Seastedt 1999), release of hormones that cue germination (Ritchie and Gilroy 1998), or the release of biologically active compounds that help break down the seed coat (Cohn 1996). Release of nutrients from decomposing plant tissue is likely the leading factor behind the stimulated emergence in this study because the boreal forest soils used are known to be nutrient-limited (Rose 2002). Alternatively, the extracts themselves may have functioned as cues indicating the existence of competition and thus inducing early germination (Preston and Baldwin 1999, Orr et al. 2005). Although many prior studies on Canada thistle allelopathy have reported a negative effect on germination of assayed crop species (Helgeson and Konzak 1950; Bendall 1975), others have reported stimulatory effects on germination by both shoot and root extracts (Béres et al. 2003;

Kazinczi et al. 2004). While even slightly accelerated tree seedling emergence rates could potentially be disadvantageous to seedlings in ecosystems where late frosts occur, as is frequently the case in Newfoundland's boreal forests, on the whole our results indicate that emergence of native tree species was not negatively affected by realistic concentrations of Canada thistle extracts. From these conclusions, the poor emergence of balsam fir in Canada thistle monocultures in natural forest gaps of Gros Morne National Park (Chapter 3) can not be attributed to allelopathy; these patterns in the field could alternatively be the result of resource-related factors or soil properties. Yet, allelopathy can not be conclusively excluded as a factor in this inhibition of emergence in the field, since here only extracts from independent sources (e.g. shoots, roots, or litter extracts independently added to thistle-derived soil) were tested, and a combination of all these sources of natural extracts may exist under field conditions.

Most prior studies of allelopathy in Canada thistle have reported negative effects on growth of other plant species (De Candolle 1832; Helgeson and Konzak 1950; Bendall 1975; Stachon and Zimdahl 1980; Wilson 1981). In this study, Canada thistle extracts did not reduce growth of balsam fir or white spruce seedlings and appears in some circumstances to have increased growth. Balsam fir seedling growth was increased by extracts of aboveground Canada thistle parts (i.e. whole shoots, minced shoots, and litter), and white spruce seedling growth was increased by the belowground Canada thistle extracts (i.e. roots and soil) and the balsam fir control extract. Similar reports of growth stimulated by Canada thistle extracts have been made by Kazinczi et al. (2004) in a bioassay on field crops. At low and biologically relevant concentrations, extracts may

sometimes encourage growth (Chon et al. 2003). These increases in growth may have again been a result of nutrients released from decaying organic compounds within the extracts (Inderjit 2001).

Although the emergence or growth of tree seedlings did not decline in the presence of Canada thistle extracts, early balsam fir and white spruce seedling survival did decrease. Balsam fir survival decreased slightly in the presence of balsam fir, whole thistle shoot, and thistle root extracts relative to the control, although only the 26.9% reduction in the survival rate by the balsam fir extract, which in fact was a 37% reduction from the rate of survival in the control, was marginally statistically significant. Spruce survival decreased in the presence of all extracts of aboveground thistle parts (i.e. whole shoots, minced shoots, and litter), although only the 29% decrease in the whole shoots treatment was statistically significant (with the other decreases being only marginally significant). Bonferroni corrections to control family-wise Type I error for this large number of *a priori* comparisons severely sacrificed statistical power (Quinn and Keough 2002), thus the estimated interpretations of statistical significance are conservative.

Two additional patterns with respect to seedling survival among extract treatments are of particular interest. Firstly, white spruce survival decreased in the presence of aboveground Canada thistle extracts, whereas belowground parts (roots and soil) and the balsam fir extract stimulated growth. A similar but opposite pattern occurred with balsam fir although it is slightly less evident: fir survival decreased in the presence of thistle root and balsam fir extracts (as well as one of the aboveground thistle extracts, i.e. whole shoots) and growth was, in contrast to spruce, increased in the presence of all

aboveground parts (i.e. whole shoots, minced shoots, and litter). Resource and non-resource (allelopathic) mechanisms (Hierro and Callaway 2003) may have both influenced the results. These results indicate that the relative effects of Canada thistle exudates from aboveground versus belowground sources on the recipient are species-specific, and suggest that Canada thistle could potentially influence community composition over time depending on the relative concentrations of each allelochemical source present in the field. As a hypothetical example, *if* native tree seedling roots uptake exudates from Canada thistle roots more consistently than from other thistle sources due to their close proximity, balsam fir survival may be more greatly affected than survival of white spruce, a subdominant species, and potential would exist for a shift in balance between native species abundance. Orr et al. (2005) point out that relatively few studies have examined the potential for a shift in native community composition if co-occurring native species respond differently to an allelopathic invader.

A second notable pattern with respect to tree seedling survival is that the largest decrease in balsam fir survival was caused by the balsam fir extract. This result is in support of other studies that have reported autotoxicity in balsam fir (Thibault et al. 1982; Singh et al. 1999) and suggests that any negative impact of Canada thistle exudates on balsam fir survival under field conditions may be less than the autotoxic effects on balsam fir by conspecifics. Survival of white spruce was not, however, significantly decreased by the balsam fir extract and thus balsam fir does not appear to exert toxic effects on this forest subdominant.

In summary, Canada thistle extracts reduced the survival of newly emerged balsam fir and white spruce seedlings by up to 23.3% and 29.7% of the survival rates in the water controls, respectively, over the first two to three months of growth. Although statistically significant only in white spruce, both tree species experienced the largest decrease in survival when receiving the whole shoot extracts. Subtle decreases in seedling survival also occurred in the roots and litter treatments. Because Canada thistle biomass usually remains on site after mechanical controls such as tilling, and this biomass has the potential to decrease survival of tree seedlings, mechanical control is not likely to be an efficient method of encouraging forest regeneration. Although not recommended in this study (see also Chapter 3), any mechanical or chemical Canada thistle control performed should, however, include measures to remove most fresh or decaying thistle biomass from the site when possible.

Experiment 2: Soil residues

Knowledge of whether residual allelochemicals in soil can impact the regeneration of native trees is critical to the development of appropriate restoration actions in thistle-invaded gaps in Gros Morne National Park. The results of experiment 2 indicate that in comparison to soil in which Canada thistle plants have not been grown (–*C.a.*), soil that recently supported a Canada thistle monoculture (+*C.a.*) does not negatively affect emergence from seed of balsam fir, white spruce, or white birch. The only significant effect of the thistle-derived soil on emergence was positive, in that balsam fir seeds planted in thistle-derived soil had increased emergence relative to non-

thistle soil. Adding activated charcoal decreased emergence in thistle-derived soils but not in non-thistle soils, suggesting that activated charcoal may have removed beneficial organic compounds from thistle-derived soil. However, when examining the effects of activated charcoal addition to soil among all the analyses, it is clear that its action in soil may have been more complex. For example, despite a lack of difference between percent birch emergence among the two soils (+*C.a.* and –*C.a.*), activated charcoal addition increased emergence 1.5 times in thistle-derived soils but cut germination in half in non-thistle soils.

Emergence time changed little for seeds grown in thistle-derived field soil relative to non-thistle soil, with a significant effect (2.1 day decrease) only found for white spruce time to emergence. As suggested for the exudates experiment (Experiment 1), this stimulated emergence rate in thistle-derived soil is likely a result of increased nutrient availability (Nilsen et al. 1999; Simons and Seastedt 1999). Again, since the addition of activated charcoal in this instance lengthened the time to emergence in non-thistle soil alone (by 2.4 days), the role of potential allelochemicals was not clear. Overall however, it is clear from these results that that any residual soil allelochemicals persisting after removal of Canada thistle do not significantly threaten the emergence of white birch, balsam fir, or white spruce seeds.

The results do, however, suggest that soil remaining after the removal of Canada thistle biomass has negative effects on early survival of native trees and thus may present an additional challenge to reestablishment of conifers in invaded gaps from seed. In both balsam fir and white spruce, survival was lower (by approximately 13% in both species)

in the thistle soil treatment than in the non-thistle soil after just 10 weeks. There was also an apparent (although statistically insignificant) negative effect of thistle-derived field soil on white spruce aboveground and belowground biomass, which was 19.4% and 28.5% higher, respectively, in non-thistle soil. Ameliorating effects of activated carbon are evidence for allelopathy (Hierro and Callaway 2003). However, the addition of activated charcoal did not improve survival success in thistle-derived soils on any occasion. It was instead found to either further decrease seedling survival in thistle soil (e.g. fir seedlings in field soil), or in the case of white spruce, cause no change to the lowered survival rates and biomass in thistle soils but decrease survival in non-thistle control soils where no effect should be expected. Therefore, the results do **not** allow determination of whether the reduced survival in thistle-derived soils is a direct result of residual allelochemicals in soil, or rather due to other soil characteristics. Species that form monospecific stands after natural or anthropogenic disturbances may significantly alter soil properties and resource availability since litter produced by these species often have different chemical ratios, nutrient mobilization processes, and decomposition rates than native plant litter (Rose and Hermanutz 2004) and may support different microbial assemblages than native vegetation (Wolfe and Klironomos 2005). Future research on the nature of this decreased survival of native trees in residual soil, and to determine the degree to which these impacts on survival persist over time (Inderjit 2001), would be beneficial in providing a better understanding of whether allelopathy or other factors drive these observed patterns.

The unanticipated effects of activated charcoal addition throughout the experiment indicate that it had an effect on seedlings independent of any potential allelochemical effect of Canada thistle. These unexpected impacts were most likely a result of reductions in nutrient availability to plants. Activated charcoal has a high affinity for organic compounds such as phytotoxic exudates (Inderjit and Callaway 2003) and a weak affinity for inorganic electrolytes such as found in nutrient solution (Cheremisinoff and Ellerbusch 1978). Although activated charcoal indiscriminately binds organics, this usually benefits native plants (Callaway and Aschehoug 2000; Ridenour and Callaway 2001; Kulmatiski and Beard 2006) because native species are likely to have evolved resistance to allelochemicals from native plants in the same region but are much more likely to be naïve to allelochemicals released by exotic plants (Bais et al. 2003; Vivanco et al. 2004). However, activated charcoal addition can sometimes reduce nutrient availability to plants when the act of sequestering organic nitrogen (N) or phosphorus (P) reduces microbial activity and decreases N and P mineralization rates (Kulmatiski and Beard 2006). Since soils in this boreal region are already nutrient-limited (Rose 2002), further decreases in nutrient availability to native trees would likely be highly detrimental. Alternatively, these independent effects of activated charcoal might have been an unrecognized result of independent changes to soil structure or composition occurring after its addition such as altered soil texture, pH, or moisture retention capabilities.

It is known that eradication of an exotic plant alone may not be followed by the return of the original community (Simberloff 2003) and belowground communities may

first need to be re-established through targeted mycorrhizae re-introductions (Wolfe and Klironomos 2005; Smith et al. 2006). For this reason, trial mycorrhizal inoculations on half of the seedlings in each treatment were performed in an effort to maximize information gain for managers about which field techniques might help to improve native seedling success in non-regenerating, Canada thistle-invaded forest gaps. The results indicate, however, that mycorrhizal inoculations did not significantly affect the time to seedling emergence, growth (i.e. shoot length and biomass), or survival for any of the tree species, and actually significantly decreased the proportion of white birch and white spruce emerging. Therefore, mycorrhizal inoculations appear to be unnecessary to facilitate establishment of balsam fir, white spruce, or white birch seeds/seedlings to boreal forest gaps in Gros Morne National Park.

There have been many recent assertions that allelopathy studies conducted in the absence of field-derived soil may not reflect activities of allelochemicals in nature (Inderjit and Dakshini 1995; Inderjit 2001). Potting soil is frequently used in growth experiments because it provides a more highly controlled and homogeneous medium than field soil, has a known composition, and also does not involve the difficult logistics of transporting large quantities of soil from often remote field locations (Hane et al. 2003). However, allelochemicals are ultimately active in actual soil systems (Inderjit and Weston 2000) and phytotoxicity of allelochemicals is highly dependent upon their movement, fate, and persistence in soil (Inderjit 2001). Allelochemicals released in soil may not reach the roots of neighboring plants in their original form, but may instead be transformed during movement, metabolized by microbes, or adsorbed to organic matter

(Inderjit 2001; Hierro and Callaway 2003). As well, allelopathic effects on neighboring plants may be dependent upon the geographical area in which they are studied (Inderjit 2001) since allelochemicals are affected by abiotic and biotic factors specific to the particular ecosystem, including soil type, temperature, pH, and microbial and mycorrhizal associations (Rice 1984; Nilsson 1994; Inderjit and Mallik 1997). Experiment 2 was repeated simultaneously within field soil and potting soil to provide a valuable opportunity to directly evaluate the variation in results among the two soils. The results revealed that patterns of emergence, growth, and survival of native tree seedlings under various soil treatments usually differed immensely between the two soils (as frequently evidenced statistically by a significant 'treatment'*'soil type' interaction and/or a significant 'soil type' variable; see Tables 4.3-4.4). This study therefore highlights the difficulty of studying field phenomenon within a substrate such as potting soil which does not accurately mimic conditions within field soil. Generally, although experiments under any greenhouse conditions can never duplicate all the complexities of field interactions and responses (Inderjit and Weston 2000; Hierro and Callaway 2003), results in field-derived soil would be expected to most closely reflect actual processes and patterns occurring in nature (Inderjit 2001).

Conclusions

Allelopathy has been described as a mechanism by which some invasive, non-native plants become dominant in recipient communities, exclude native species, and often form monospecific stands (Ridenour and Callaway 2001; Hierro and Callaway

2003; Levine et al. 2003). Allelopathy by native or non-native plants has also often been implicated as a factor in forest regeneration failures or delays (Gabriel 1975; Fisher 1980; Rice 1984). In boreal forests, perhaps the best-studied examples of allelopathy causing regeneration failures involve inhibition of trees by various shrubs. In Newfoundland, allelopathy by sheep laurel (*Kalmia angustifolia* L.) has been shown to be a major factor in the inhibition of black spruce (Mallik 1987; Yamasaki et al. 1998). In the southeastern United States, Skulman et al. (2004) suggest that Japanese honeysuckle (*Lonicera japonica* Thunb.) prevents regeneration of loblolly (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) species partially through allelopathic effects of its leaf litter in the soil. The germination and growth of Scots pine (*Pinus syvestris* L.) in Sweden has been attributed to inhibition by crowberry (*Empetrum hermaphorditum* Hagerup) (Zackrisson and Nilsson 1992) and similarly, regeneration failure of Norway spruce (*Picea abies* (L.) Karst) in subalpine forests in France has been attributed to allelopathic effects of phenolic compounds from bilberry (*Vaccinium myrtillus* L.) on spruce germination and seedling growth (Pellissier 1993; Souto et al. 2000). Allelopathy from herbaceous plants on tree seedlings has also been shown to inhibit succession in old fields (Fisher 1980; Rice 1984; Ponder 1986). For example, Fisher et al. (1978) suggests that exudates from goldenrod (*Solidago canadensis* L., *S. graminifolia* (L.) Salisb.) and aster (*Aster novae-algliae* L.) inhibit germination and early growth of sugar maple (*Acer saccharum* Marsh) in old fields. The present study is unique in that it examines the potential for large-scale allelopathic inhibition of native tree regeneration within a protected boreal forest by an exotic weed whose invasive presence is highly uncharacteristic within the study system.

Knowledge of the potential role of allelopathy in causing regeneration failures is vital since without this knowledge, managers of natural areas may attempt remedies that are unnecessarily costly or heavy handed, even when they succeed (Fisher 1980).

This research provides evidence that realistic exudates from Canada thistle exhibit allelopathic interference of early seedling survival of balsam fir and white spruce, two of the most dominant tree species in Gros Morne National Park and throughout the boreal forests of northeastern North America. Thus, Canada thistle invasion into boreal forests gaps may threaten natural regeneration of these native species by exerting harmful allelopathic effects on the survival of new emergents. The results also showed that balsam fir and white spruce seedlings growing in soil that previously supported dense Canada thistle growth experienced lowered survival than those in soil not previously invaded by thistle, although it was not possible to confirm or exclude the role of allelopathy in driving this pattern. Early germination and growth of the native trees do not appear to be similarly affected and even demonstrated some evidence of growth stimulation by Canada thistle. Since the relative effects of various extracts from aboveground and belowground Canada thistle sources on survival and growth of recipient native trees was species-specific, and since the natural occurrence of exudates from either source may vary under field conditions and differentially affect the survival of native tree seedlings, even small imbalances in early native seedling success could potentially lead to larger-scale influences on community composition over time. Taking this potential impact of Canada thistle into consideration will be valuable during any restoration efforts and adaptive management within forest gaps in Gros Morne National Park, particularly

since browsing by hyperabundant moose is already strongly shifting community composition through decreases in the palatable white birch and balsam fir abundance and increases in unpalatable white spruce (Forbes 2006).

Results of these greenhouse studies provide clues about the effects of Canada thistle on native tree species but can not be assumed to directly mimic complex field conditions. For instance, despite the finding that Canada thistle can exert negative effects on early balsam fir survival over the first two months after emergence, under field conditions in Gros Morne National Park's forest gaps, newly emerged balsam fir seedlings were reported to experience higher survival within Canada thistle monocultures than in uninvaded areas over the first summer growing season (Chapter 3). This was due to protection that the sharp thistle spines provided from browsing herbivores, and the pattern declined over two years until no surviving fir seedlings remained within the thistle monocultures (Chapter 3). Yet these results in the field do not contradict the findings that thistle exudates may lower native seedling survival during the first weeks after emergence. Rather, under these specific field conditions, external influences of browsers on early seedling survival clearly outweigh any potential allelochemical impacts, particularly since conifer seedlings are at greatest risk of predation during the first 10-16 weeks post-germination (Duchesneau and Morin 1999; Noel 2004). Ultimately, a large number of interacting factors and tradeoffs will determine success of native plants under field conditions, but knowledge of the role of allelopathy in explaining observed outcomes is invaluable to better understanding community dynamics and developing realistic and effective management strategies.

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Table 4.1 – *A priori* contrasts performed to test three specific hypotheses upon the finding of a significant treatment effect in Experiment 2, and the expected results of these contrasts if hypotheses are correct. Contrasts were Bonferroni corrected for three comparisons ($\alpha' = 0.0167$). AC = activated charcoal; *+C.a.* = soil that supported previous growth of *Cirsium arvense*; *–C.a.*= soil that did not support *C.arvense*. AC subscript on *+C.a.* or *–C.a.* indicates that activated charcoal was added to the soil.

Hypotheses	**Contrast**	**Expected results and conclusions**
1. Native tree success in soil originating from a thistle monoculture is lower than in soil that did not previously support growth of thistle	*+C.a.* vs. *–C.a.*	Significant contrast; lower success in *+C.a.* soil; conclude there is a negative impact of Canada thistle on native tree species
2. Adding AC to soil removed from underneath thistle monocultures will increase seedling success	*+C.a.* vs. $+C.a._{AC}$	Significant contrast; increased success in $+C.a._{AC}$ relative to *+C.a.*; conclude Canada thistle exerts an allelopathic effect on native tree species
3. Adding AC to soil not previously supporting thistle will not significantly affect the success of native tree seedlings (i.e. a control for AC application)	*–C.a.* vs. $-C.a._{AC}$	Insignificant contrast; conclude there is no independent effect of adding AC in the absence of potential Canada thistle allelochemicals

Table 4.2 – Statistical results from a MANOVA and univariate ANOVAs examining the fixed effects of various aqueous extracts (i.e. treatment), tree species, and the treatment×species interaction on the aboveground and belowground biomass of balsam fir and white spruce seedlings harvested 10 weeks after seed planting. Biomass of white birch has been excluded from the analysis due to disproportionate browsing on this species, making differentiation of treatment versus external effects on biomass difficult.

Effect	**MANOVA**				**ANOVA (univariate)**							
	Biomass				**Aboveground Biomass**				**Belowground Biomass**			
	Wilk's Lambda	**df**	**F**	**p**	**MS ($\times 10^{-4}$)**	**df**	**F**	**p**	**MS ($\times 10^{-4}$)**	**df**	**F**	**p**
Main model:												
Treatment	0.91082	12,52	2.10	**0.0153**	0.8507	6,265	2.37	**0.0299**	0.0969	6,265	1.35	0.2339
Species	0.79208	2,264	34.65	**<.0001**	6.0065	1,265	16.76	**<.0001**	4.1428	1,265	57.84	**<.0001**
Treatment*Species	0.87831	12,52	2.95	**0.0005**	1.2767	6,265	3.56	**0.0021**	0.2117	6,265	2.96	**0.0083**
By species:												
Balsam fir:												
Treatment	0.75513	12,26	3.32	**0.0002**	1.2166	6,133	3.36	**0.0041**	0.1846	6,133	1.76	0.1129
White spruce:												
Treatment	0.79191	12,26	2.70	**0.0019**	0.9218	6,132	2.60	**0.0207**	0.1237	6,132	3.27	**0.0050**

p-values ≤ 0.05 are shown in bold face

Table 4.3 – Statistical results from generalized linear models examining the fixed effects of treatment (Trt), mycorrhizal addition (Mycorr), soil type (Soil), and all their possible interactions on emergence (binomial error), days to emergence (Poisson error), and survival (binomial error) of various tree species. Survival of white birch has been excluded from the analysis due to disproportionate browsing on this species, making differentiation of treatment versus external effects on survival difficult.

Effect	Emergence (%)			Days to Emergence			Survival (%)		
	df	χ^2	p	df	χ^2	P	df	χ^2	p
White birch									
Trt	3	28.25	**<.0001**	3	8.00	**0.0460**	-	-	-
Mycorr	1	18.40	**<.0001**	1	1.08	0.2978	-	-	-
Soil	1	2.39	0.1221	1	1.54	0.2152	-	-	-
Trt * Mycorr	3	8.62	**0.0348**	3	1.41	0.7041	-	-	-
Trt *Soil	3	22.89	**<.0001**	3	5.50	0.1387	-	-	-
Mycorr * Soil	1	0.09	0.7605	1	0.58	0.4453	-	-	-
Trt * Mycorr *Soil	3	1.37	0.7125	3	15.27	**0.0016**	-	-	-
Balsam fir									
Trt	3	7.81	**0.0500**	3	3.72	0.2937	3	7.71	***0.0524***
Mycorr	1	0.00	0.9923	1	0.20	0.6554	1	2.53	0.1115
Soil	1	0.65	0.4200	1	26.28	**<.0001**	1	3.01	0.0826
Trt * Mycorr	3	2.49	0.4772	3	1.10	0.7769	3	2.78	0.4260
Trt * Soil	3	3.16	0.3682	3	10.00	**0.0186**	3	14.80	**0.0020**
Mycorr * Soil	1	2.09	0.1481	1	0.01	0.9322	1	0.23	0.6297
Trt * Mycorr * Soil	3	4.99	0.1722	3	6.52	0.0889	3	3.41	0.3321
White spruce									
Trt	3	3.19	0.3627	3	5.12	0.1632	3	8.71	**0.0335**
Mycorr	1	6.15	**0.0131**	1	0.00	0.9958	1	1.01	0.3151
Soil	1	0.18	0.6725	1	1.54	0.2152	1	14.99	**0.0001**
Trt * Mycorr	3	3.09	0.3781	3	0.81	0.8479	3	2.77	0.4291
Trt * Soil	3	4.90	0.1789	3	11.68	**0.0086**	3	1.34	0.7193
Mycorr * Soil	1	3.28	0.0700	1	0.09	0.7600	1	0.28	0.5938
Trt * Mycorr *Soil	3	0.25	0.9689	3	0.65	0.8854	3	3.15	0.3689

p-values ≤ 0.05 are shown in bold face.

Table 4.4 – Statistical results from a MANOVA examining the fixed effects of treatment (Trt), mycorrhizal addition (Mycorr), soil type (Soil), and all their possible interactions on aboveground and belowground biomass of balsam fir and white spruce seedlings harvested 10 weeks after seed planting. Biomass of white birch has been excluded from the analysis due to disproportionate browsing on this species, making differentiation of treatment versus external effects on biomass difficult.

Effect	MANOVA				ANOVA (univariate)							
	Biomass				Aboveground Biomass				Belowground Biomass			
	Wilk's Lambda	df	F	p	MS ($\times 10^{-4}$)	df	F	p	MS ($\times 10^{-4}$)	df	F	p
Balsam fir												
Trt	0.954	6,284	1.14	0.3395	0.4624	3,143	1.79	0.1521	0.1224	3,143	1.65	0.1815
Mycorr	0.991	2,142	0.64	0.5271	0.2226	1,143	0.86	0.3551	0.0081	1,143	0.11	0.7421
Soil	0.867	2,142	10.93	**<.0001**	5.5279	1,143	21.38	**<.0001**	1.2754	1,143	17.15	**<.0001**
Trt * Mycorr	0.974	6,284	0.64	0.7000	0.1039	3,143	0.40	0.7519	0.0363	3,143	0.49	0.6914
Trt * Soil	0.947	6,284	1.31	0.2537	0.4410	3,143	1.71	0.1686	0.1504	3,143	2.02	0.1135
Mycorr * Soil	0.985	2,142	1.05	0.3529	0.0501	1,143	0.19	0.6604	0.0186	1,143	0.25	0.6176
Trt * Mycorr * Soil	0.937	6,284	1.56	0.1584	0.5053	3,143	1.95	0.1236	0.0274	3,143	0.37	0.7759
White spruce												
Trt	0.954	6,284	1.13	0.3464	0.1398	3,143	1.48	0.2217	0.0605	3,143	2.14	0.0978
Mycorr	0.998	2,142	0.12	0.8913	0.0208	1,143	0.22	0.6396	0.0015	1,143	0.05	0.8187
Soil	0.816	2,142	16.00	**<.0001**	2.7605	1,143	29.29	**<.0001**	0.1484	1,143	5.25	**0.0234**
Trt * Mycorr	0.890	6,284	2.83	**0.0108**	0.3481	3,143	3.69	**0.0134**	0.1123	3,143	3.97	**0.0094**
Trt * Soil	0.902	6,284	2.50	**0.0225**	0.1548	3,143	1.64	0.1822	0.1207	3,143	4.27	**0.0064**
Mycorr * Soil	0.972	2,142	2.02	0.1364	0.2286	1,143	2.43	0.1216	0.1121	1,143	3.97	**0.0483**
Trt * Mycorr * Soil	0.968	6,284	0.79	0.5798	0.0107	3,143	0.11	0.9518	0.0182	3,143	0.64	0.5891

p-values ≤ 0.05 are shown in bold face.

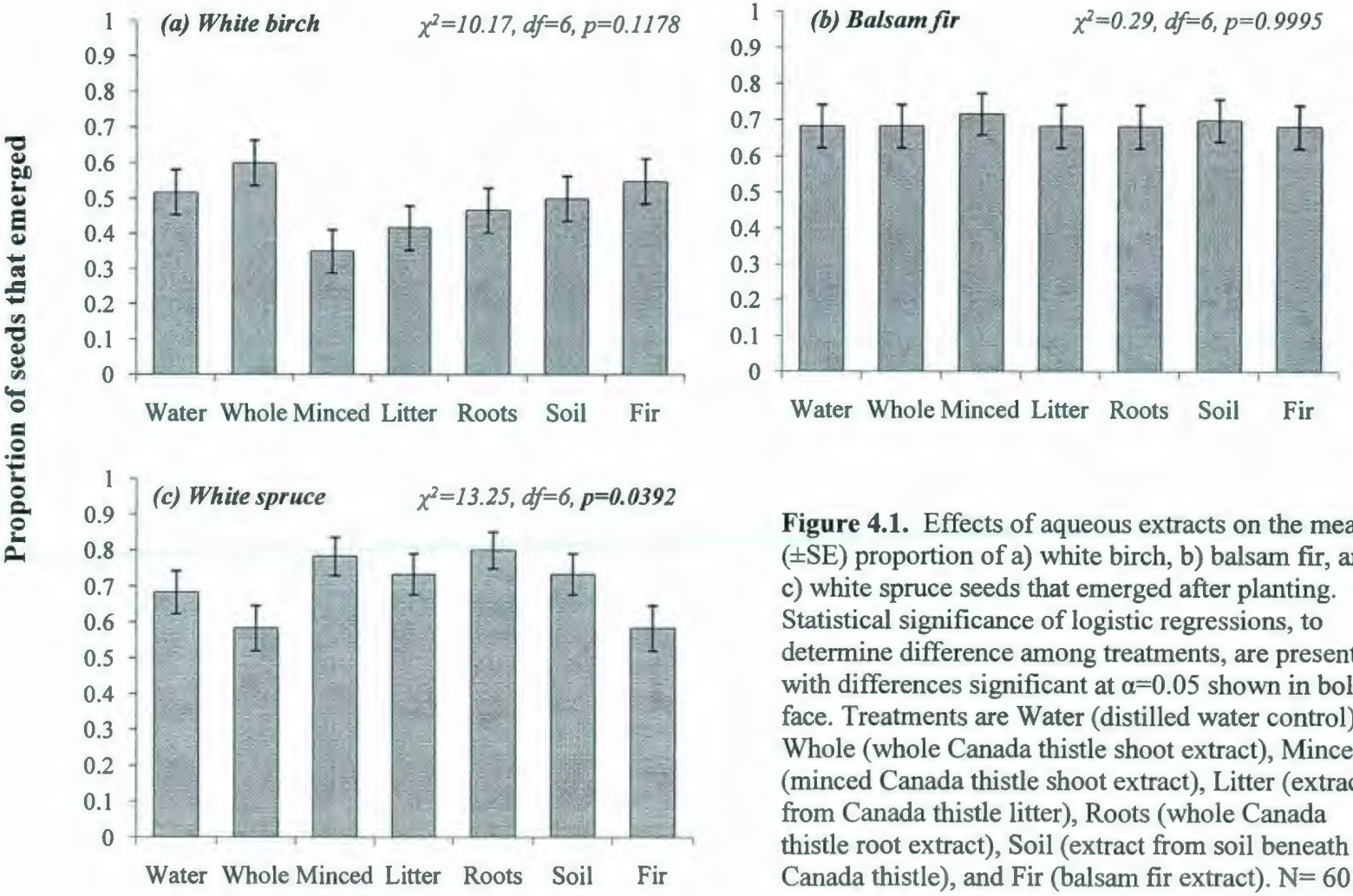


Figure 4.1. Effects of aqueous extracts on the mean (±SE) proportion of a) white birch, b) balsam fir, and c) white spruce seeds that emerged after planting. Statistical significance of logistic regressions, to determine difference among treatments, are presented with differences significant at α=0.05 shown in bold face. Treatments are Water (distilled water control), Whole (whole Canada thistle shoot extract), Minced (minced Canada thistle shoot extract), Litter (extract from Canada thistle litter), Roots (whole Canada thistle root extract), Soil (extract from soil beneath Canada thistle), and Fir (balsam fir extract). N= 60 seeds per treatment.

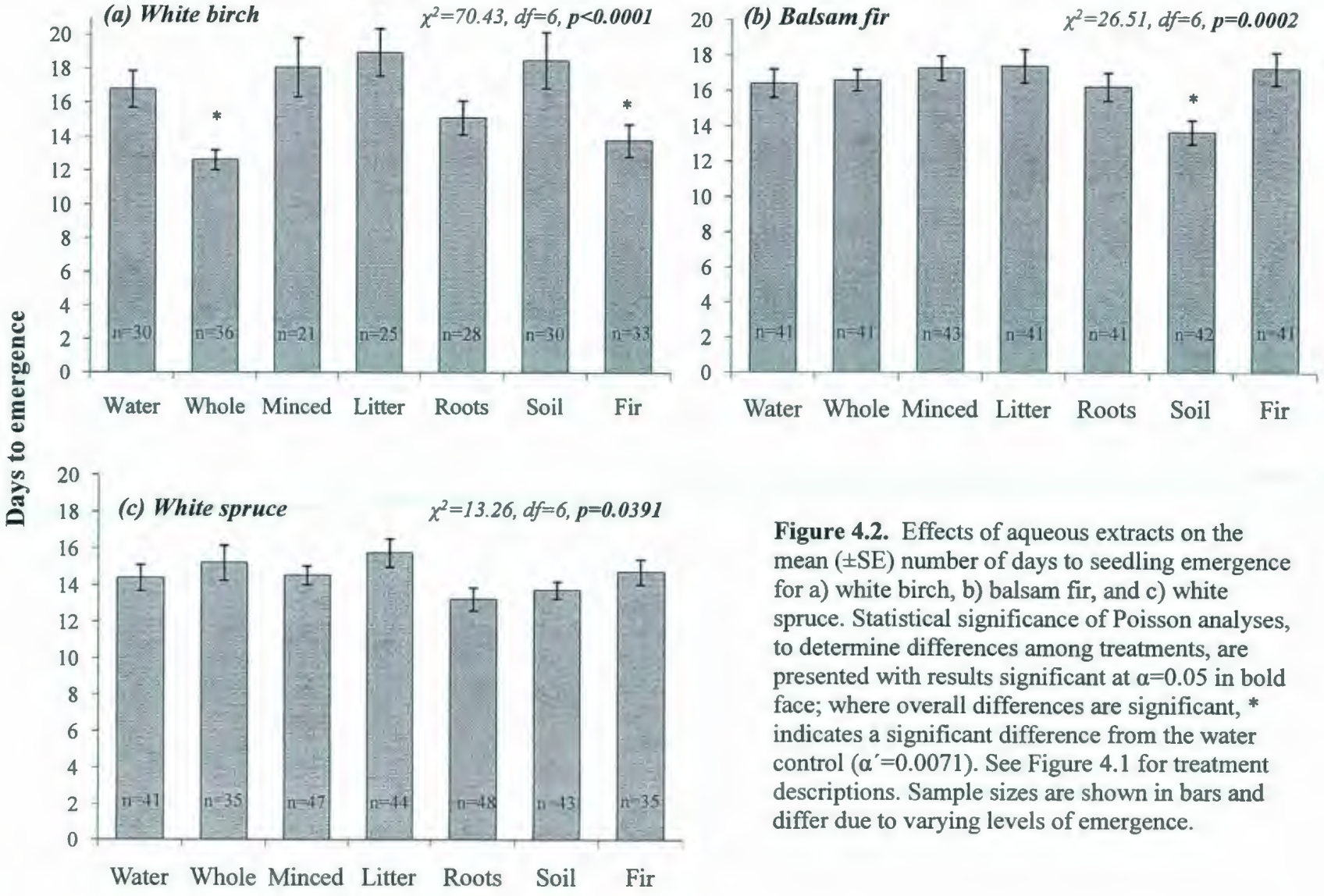


Figure 4.2. Effects of aqueous extracts on the mean (±SE) number of days to seedling emergence for a) white birch, b) balsam fir, and c) white spruce. Statistical significance of Poisson analyses, to determine differences among treatments, are presented with results significant at α=0.05 in bold face; where overall differences are significant, * indicates a significant difference from the water control (α'=0.0071). See Figure 4.1 for treatment descriptions. Sample sizes are shown in bars and differ due to varying levels of emergence.

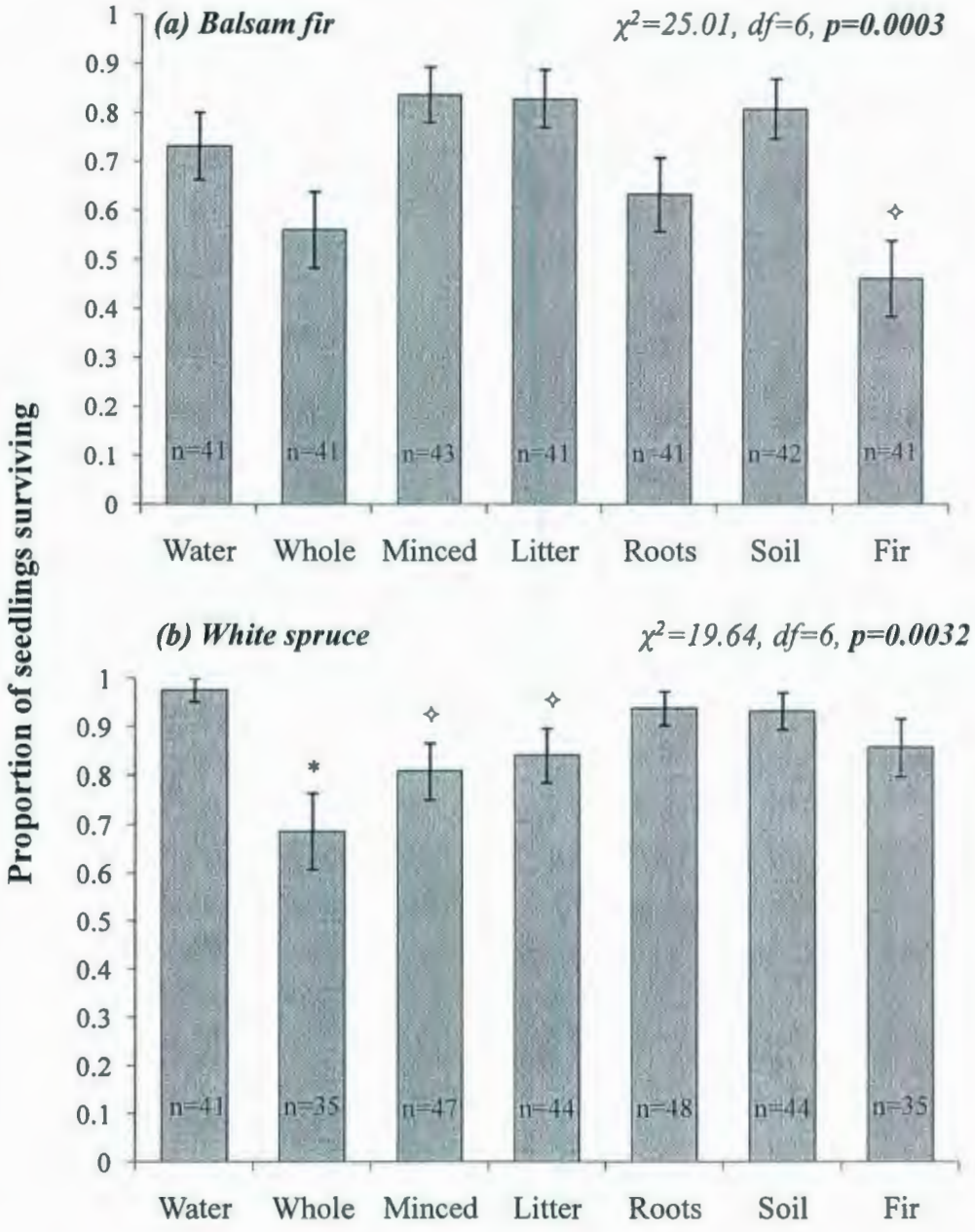


Figure 4.3. Effects of aqueous extracts on the mean (±SE) proportion of (a) balsam fir, and (b) white spruce seedlings that survived a 10 week experimental period. Statistical significance of logistic regressions, to determine difference among treatments, are presented with differences significant at α=0.05 shown in bold face. Where overall differences are significant, * indicates a significant difference from the water control (α'=0.0071) and ✧ indicates a marginally significant difference from the control (i.e. if $p<0.05$). See Figure 4.1 for treatment descriptions. Sample sizes are given on bars in graph and differ due to varying initial emergence.

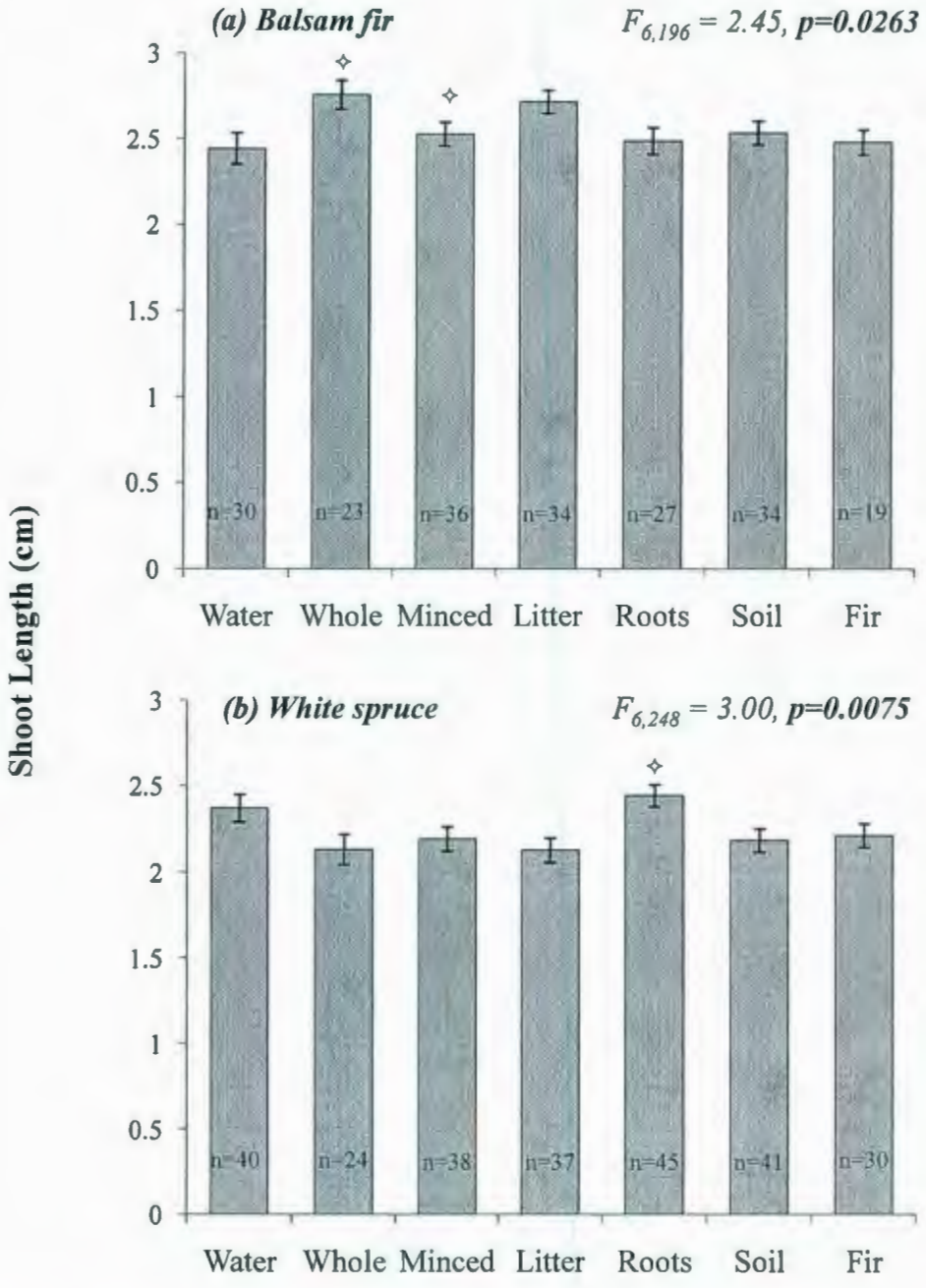


Figure 4.4. Effects of aqueous extracts on the mean (±SE) shoot length of a) balsam fir, and b) white spruce seedlings 10 weeks after planting seeds. Statistical significance of ANOVAs, to determine difference among treatments, are presented with differences significant at α=0.05 shown in bold face. Although there is a significant treatment effect in both balsam fir and white spruce, no treatments are statisticaly significant from the water control (at α'=0.0071). A ✧ indicates a marginally significant difference from the control (i.e. $p<0.05$). See Figure 4.1 for treatment descriptions. Sample sizes are given in bars and differ due to varying initial emergence.

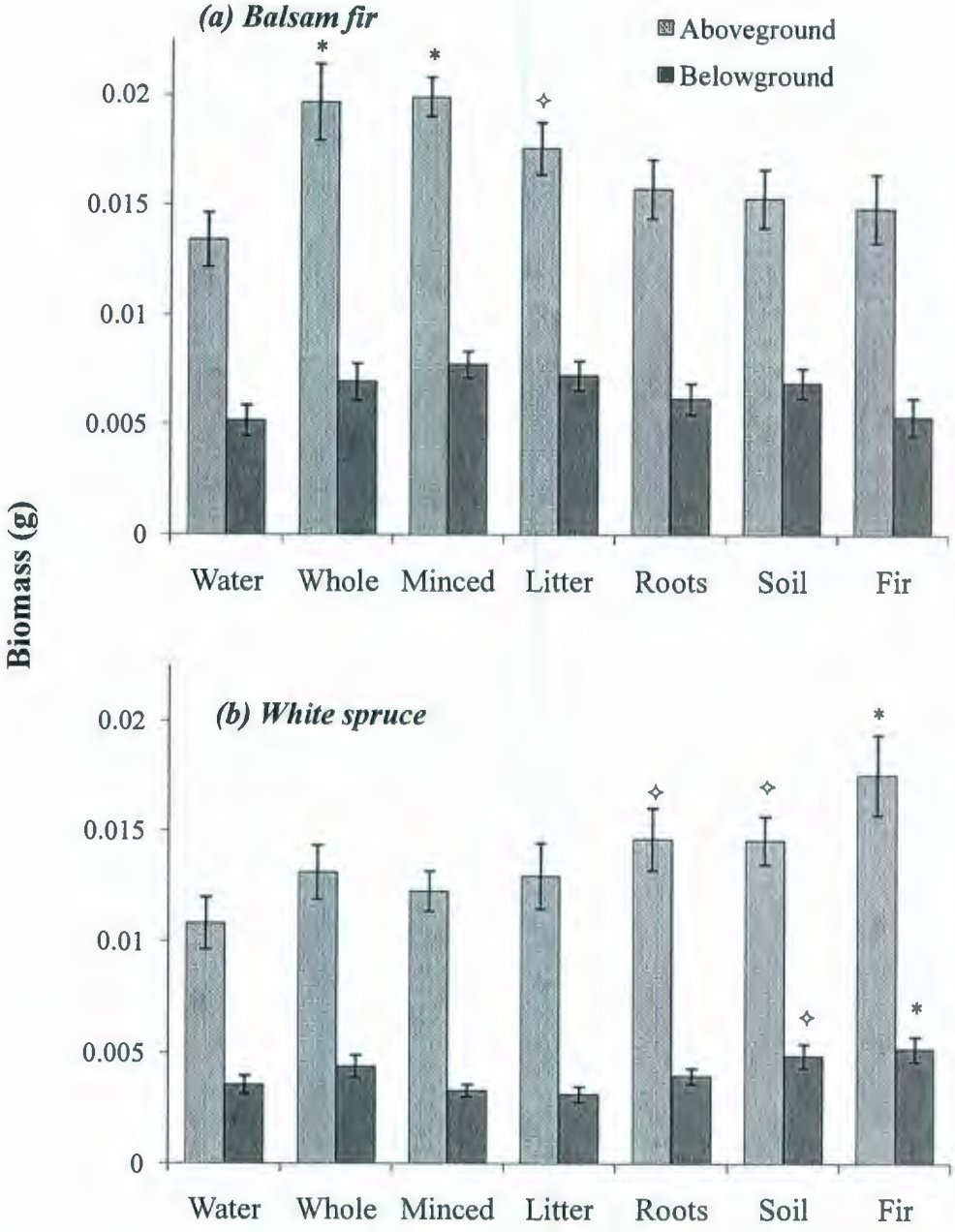
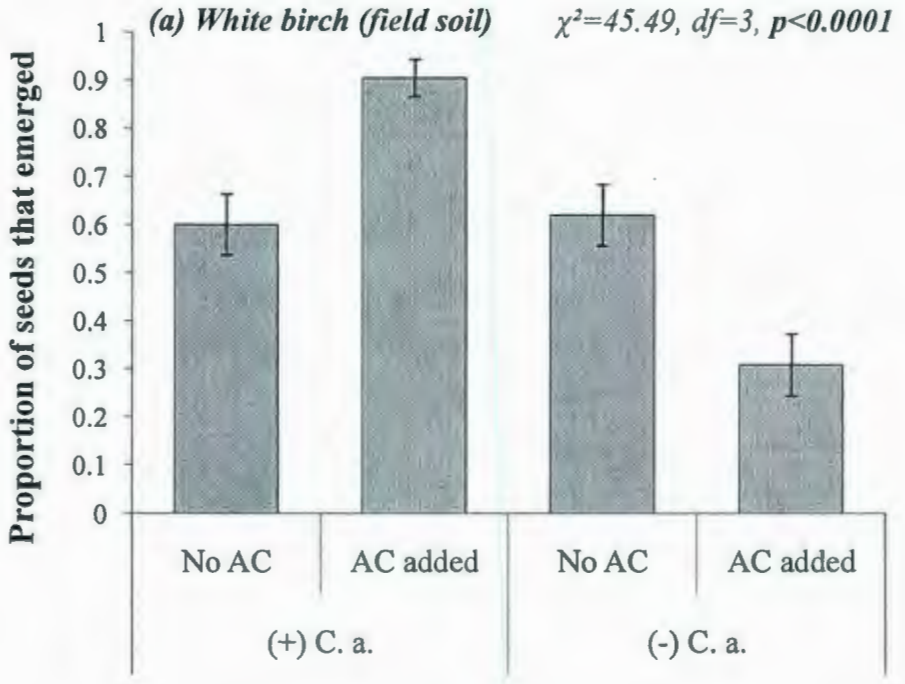
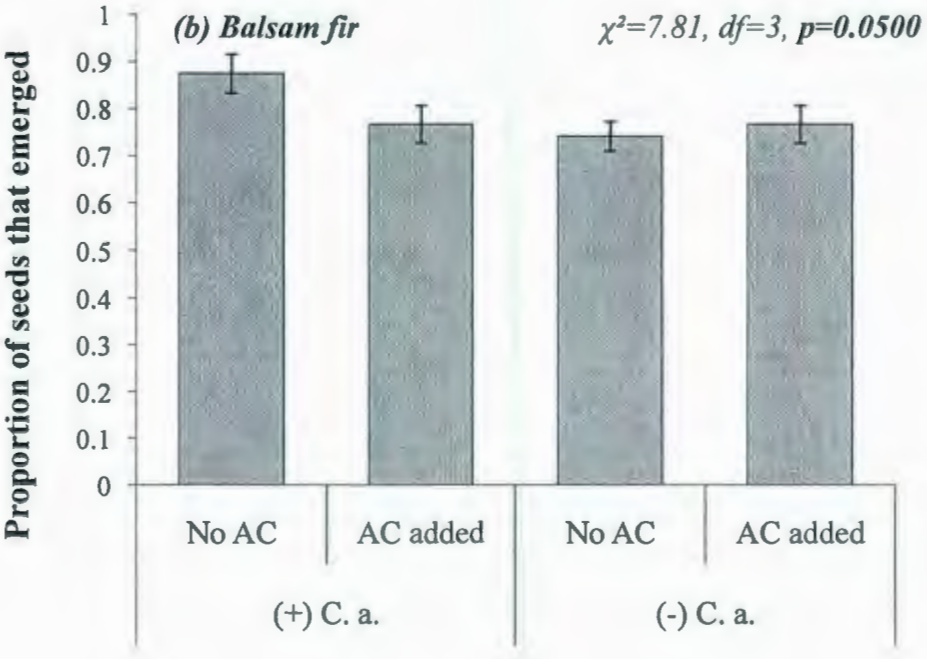


Figure 4.5. Effects of aqueous extracts on the mean (±SE) dry above- and below-ground biomass of a) balsam fir, and b) white spruce seedlings harvested 10 weeks after planting seeds. Statistical significance of MANOVAs and univariate ANOVAs, to determine difference among treatments, are presented in Table 4.1 and are not repeated here. Where overall differences are significant, * indicates a significant difference from the water control ($\alpha'=0.0071$) and ✧ indicates a marginally significant difference from the control (i.e. if $p<0.05$). See Figure 4.1 for treatment descriptions. N=20 seedlings of each tree species per treatment.





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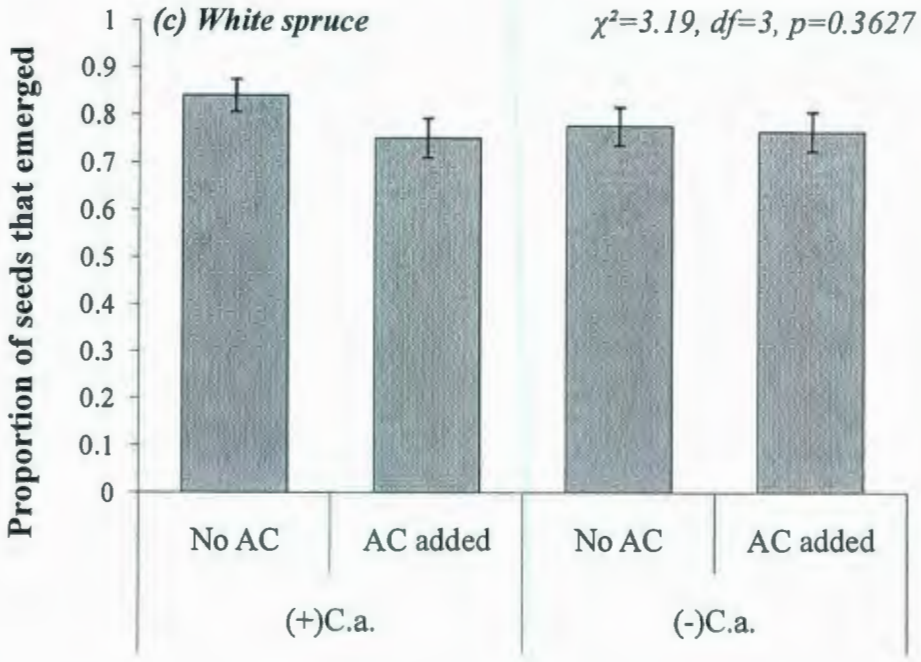

Figure 4.6 - Effects of previous Canada thistle growth in soil and activated charcoal addition to soil on mean (±SE) proportion of seeds emerging for a) white birch planted in field-derived soil, b) balsam fir (combined field-derived soil and potting soil), and c) white spruce (combined soils). In a), each bar represents n= 60 seeds. In b) and c), each bar represents n=120 seeds. AC = activated charcoal; (+) *C.a.* = soil that supported previous growth of *Cirsium arvense*; (-) *C.a.* = soil that did not support growth of *C. arvense*. Statistical significance of logistic regressions, to determine difference among treatments, are presented with differences significant at α=0.05 shown in bold face.

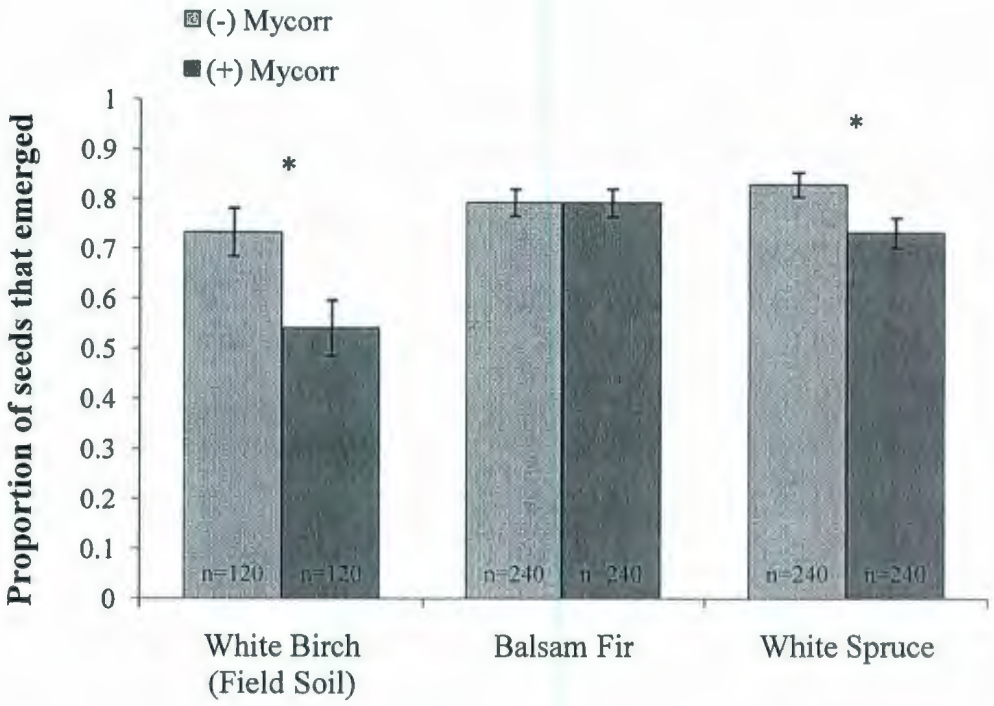

Figure 4.7 – Effects of soil mycorrhizal inoculation on mean (±SE) emergence of white birch, balsam fir, and white spruce seeds. Light bars = no mycorrhizal addition (-) ; dark bars = mycorrhizal addition performed (+). Bars for balsam fir and white spruce indicate seeds planted in field soil and potting soil combined; in white birch, emergence is shown in field soil only due to interactive effects of soil type (Table 4.2). A * indicates a significant difference between (-) mycorrhizae and (+) mycorrhizae conditions at $\alpha = 0.05$ within any species. Sample sizes are shown in bars.

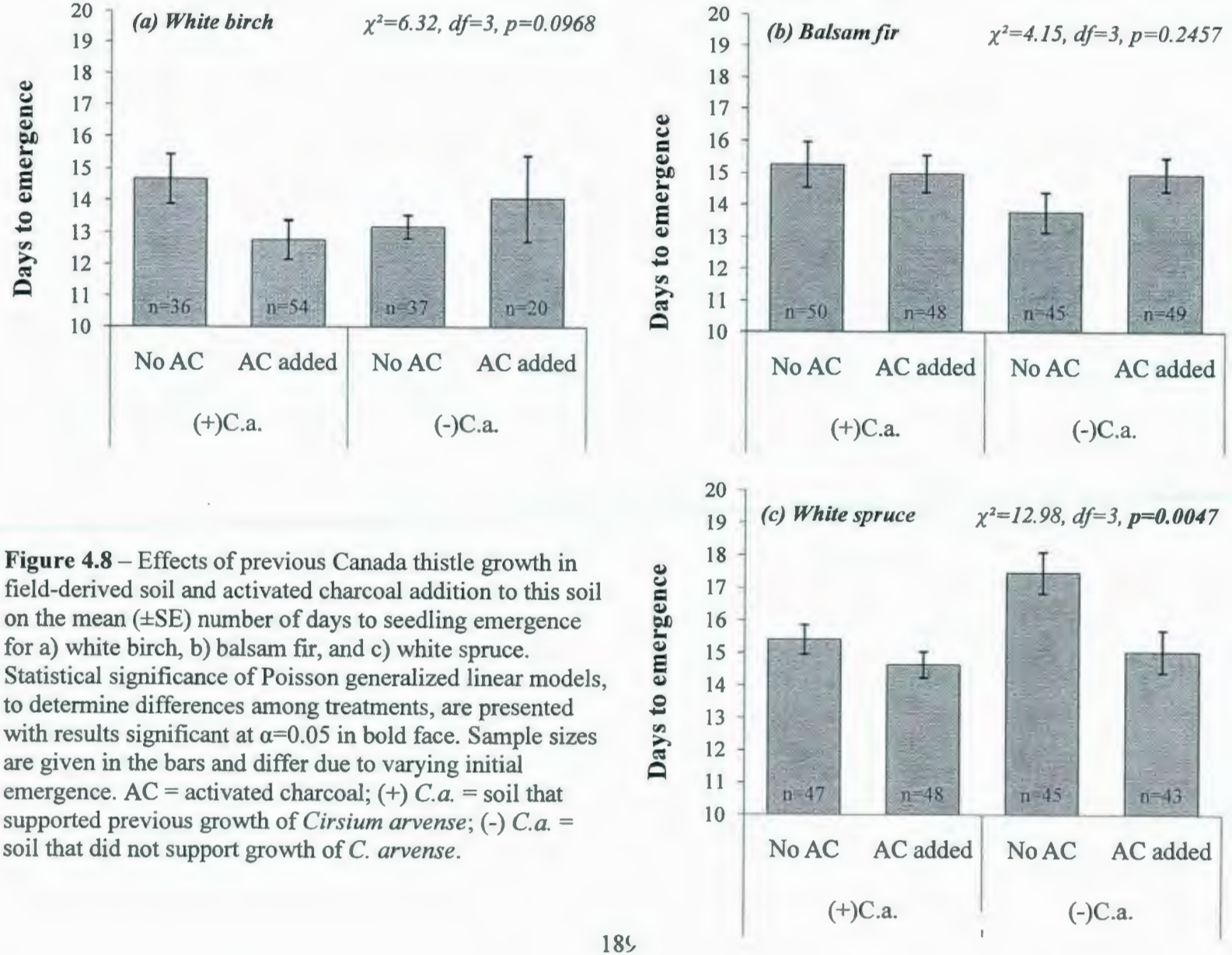

Figure 4.8 – Effects of previous Canada thistle growth in field-derived soil and activated charcoal addition to this soil on the mean (±SE) number of days to seedling emergence for a) white birch, b) balsam fir, and c) white spruce. Statistical significance of Poisson generalized linear models, to determine differences among treatments, are presented with results significant at α=0.05 in bold face. Sample sizes are given in the bars and differ due to varying initial emergence. AC = activated charcoal; (+) *C.a.* = soil that supported previous growth of *Cirsium arvense*; (-) *C.a.* = soil that did not support growth of *C. arvense*.

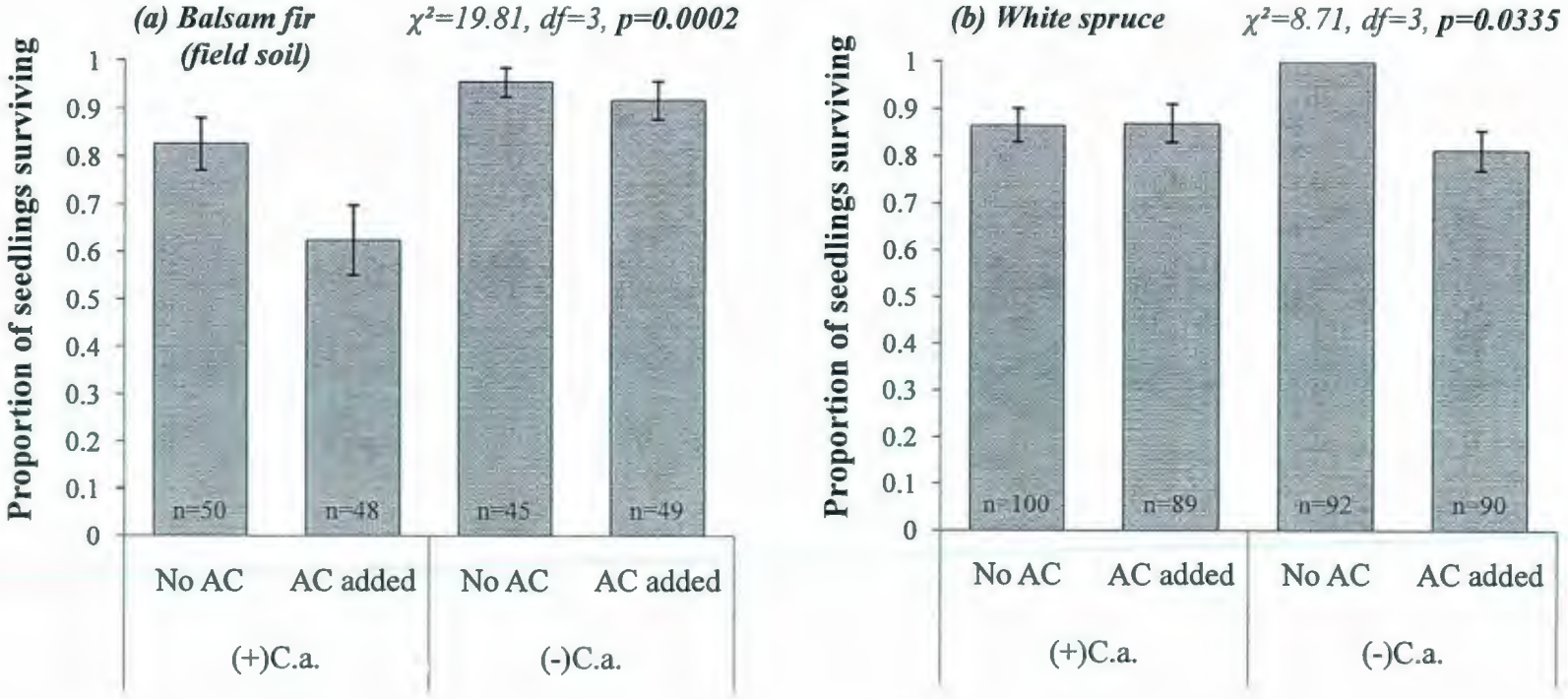

Figure 4.9 – Effects of previous Canada thistle growth in soil and activated charcoal addition to soil on the mean (±SE) survival of a) balsam fir seedlings in field soil, and b) white spruce seedling (field and potting soil combined) over a 10 week experimental period. Statistical significance of logistic regressions, to determine difference among treatments, are presented with differences significant at $\alpha=0.05$ shown in bold face. Sample sizes are given in the bars and differ due to varying initial emergence. AC = activated charcoal; (+) *C.a.* = soil that supported previous growth of Canada thistle; (-) *C.a.* = soil that did not support thistle.

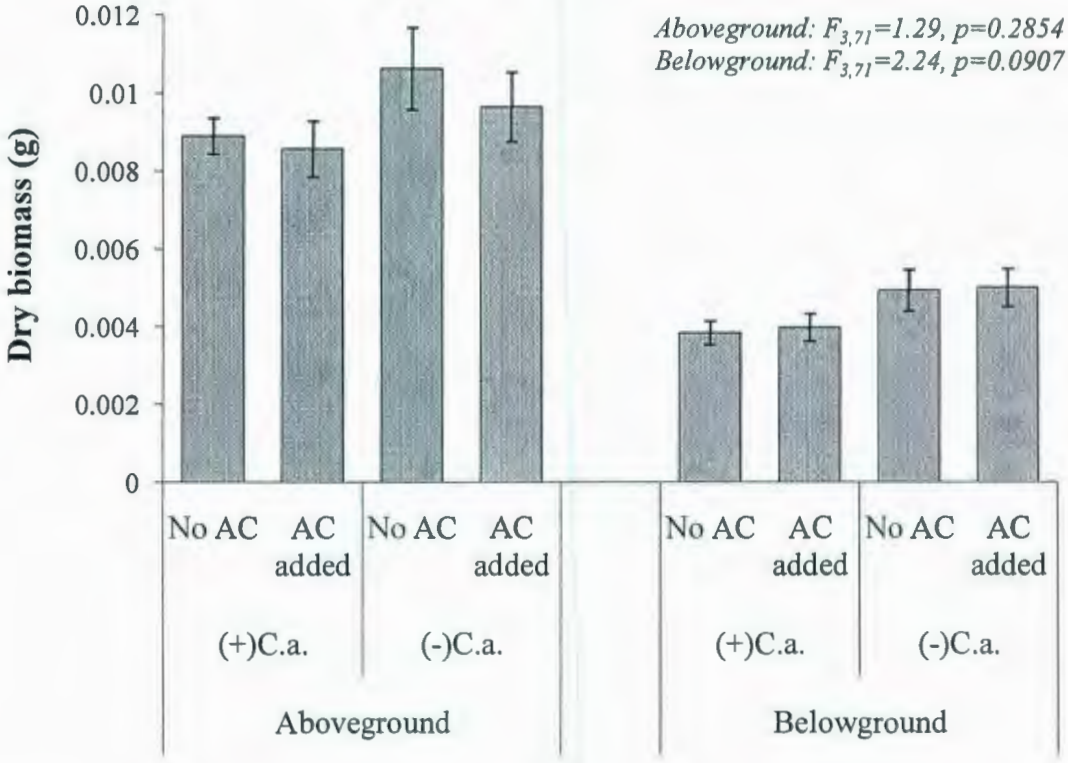

Figure 4.10 – Effects of previous Canada thistle growth in soil and activated charcoal addition to soil on the mean (±SE) aboveground and belowground dry biomass of white spruce seedlings in field soil. Seedlings were harvested for determination of biomass 10 weeks after planting of seeds. Each bar represents n=20 seedlings. AC = activated charcoal; (+) *C.a.* = soil that supported previous growth of *Cirsium arvense*; (-) *C.a* = soil that did not support *C. arvense*. Results of univariate ANOVAs, to determine biomass differences among treatments, are shown.

5. SUMMARY AND CONCLUSIONS

This study describes the severity of the forest regeneration failure occurring throughout natural and anthropogenic boreal forest gaps of Gros Morne National Park, and investigates the impact of non-native Canada thistle infestations within these gaps on emergence, growth, and survival of balsam fir (the dominant tree species) as well as two subdominant tree species (i.e. white spruce and white birch). The results support habitat management aimed at preventing further forest degradation and restoring ecological integrity within gaps that have been altered dramatically by moose overbrowsing and alien plant invasion.

Through use of vegetation surveys, the research presented in Chapter 2 reveals that densities of regenerating balsam fir (i.e. < 1 individual per m^2) within naturally- and anthropogenically- disturbed forest gaps in Gros Morne National Park are much lower than levels of regeneration expected for this region under lower moose densities. These densities would be insufficient to adequately re-stock forest gaps. In natural gaps, the apical meristem of over 98% of fir >30 cm in height was browsed at least once, and usually numerous times; apical meristem browsing levels were only slightly lower in anthropogenic gaps, at just over 92%. Where balsam fir does occur, it is highly stunted (almost always < 1 m) from sustained browsing pressure and, as a result, is prevented from reaching adult reproductive stages or forming a canopy. In Chapter 2 it was also shown that seedbeds within these natural and anthropogenic gaps consist predominantly of highly unfavourable substrates for conifer recruitment (i.e. alien and native herbaceous weeds, as well as shrubs and grasses). As seedbed quality largely determines success of

balsam fir at the germination and early establishment stages (Calogeropoulos et al. 2004), the poor condition of seedbeds in GMNP will further reduce future regeneration potential within gaps. Invasion of gaps by herbaceous non-native plant species presents additional challenges for Park managers. In particular, invasion by Canada thistle has occurred on a widespread landscape scale, with approximately half of all gaps surveyed containing dense thistle patches.

Through experimental additions of balsam fir seeds and seedlings (aged 15 months) into non-regenerating gaps, Chapter 3 illustrates that invasion of non-native Canada thistle into boreal forest gaps negatively impacts balsam fir regeneration at the early stages of emergence and survival. These impacts may potentially impede natural balsam fir regeneration independent of changes in moose densities. In natural forest gaps, emergence of balsam fir was greatly lowered in monocultures of Canada thistle relative to uncolonized areas of the gaps. Removing aboveground, or above- and belowground, Canada thistle biomass through cutting and digging did not significantly improve emergence. This suggests that the inhibition might not have been a result of direct competition from Canada thistle, but rather may have been due to direct or indirect allelopathic effects in the soil which can remain after physical removal of the invader (Bendall 1975, Stowe 1979, Wilson 1981). However, since emergence was almost nil throughout anthropogenic gaps, regardless of whether seeds were planted amongst Canada thistle or a favourable native seedbed, this research highlights a serious problem with recruitment limitation under this disturbance regime, regardless of the status of

Canada thistle invasion. Further research is needed to investigate the cause of this ubiquitously low emergence within anthropogenic gaps.

The results of Chapter 3 also indicate that survival of newly emerging balsam fir seedlings is negatively affected by Canada thistle; none of the seedlings that emerged within thistle monocultures survived to their second year, regardless of whether thistle biomass was removed or left intact. This result supports the role of allelopathy as a likely mechanism of interference. This experiment also revealed that a tradeoff may exist for newly emerged seedlings growing among thistle: there may be a net benefit on seedlings at early stages when the seedling is most vulnerable to herbivory, since the sharp thistle spines deterred browsing herbivores, but, over time, negative impacts on survival ultimately outweigh any benefits.

Allelopathy experiments conducted in a greenhouse (Chapter 4) further clarified the role of allelopathy (through either direct or indirect action) in explaining these patterns of balsam fir interference within the field. While emergence of native tree species (i.e. balsam fir, white birch, and white spruce) was not negatively affected by concentrations of Canada thistle extracts that aimed to simulate naturally-occurring exudates, or by growing in soil that previously supported a Canada thistle monoculture, early survival of newly emerged balsam fir and white spruce seedlings was reduced in both cases. Realistic concentrations of Canada thistle exudates lowered the survival of balsam fir and white spruce seedlings by up to 23% and 30% compared with the deionized water control, respectively, over the first few 2-3 months. Canada thistle shoots showed the greatest allelopathic potential, but inhibitory effects of roots and litter were

also noted. The relative effects of various extracts from aboveground and belowground Canada thistle sources on survival and growth of recipient native trees was species-specific, suggesting that allelopathy from Canada thistle could influence native community composition differentially over time, depending on the sources of exudates present under field conditions. In addition, balsam fir and white spruce seedlings growing in soil that previously supported dense Canada thistle growth experienced lowered survival (i.e. 13% lower after 10 weeks in both species) than those in soil not previously invaded by thistle, although it was not possible to confirm or exclude the role of allelopathy in determining this pattern.

The results from these allelopathy experiments strengthen the assertion that low early survival of balsam fir among Canada thistle monocultures under field conditions may be partly due to harmful allelopathic effects from the non-native invader. The role of allelopathy in contributing to the poor emergence of balsam fir in thistle monocultures in the field can not be confirmed, since neither extracts from Canada thistle or thistle-derived soil was found to reduce emergence; observed patterns in the field may have been the result of resource-related factors, competition from remaining roots in soil, or other soil properties. However, a role for allelopathy in this inhibition of emergence in the field can not be excluded, since only extracts from independent sources (e.g. shoots, roots, or litter extracts independently added to thistle-derived soil) were tested, and a combination of all these sources of natural extracts may exist under field conditions. It is clear, however, that Canada thistle invasion into boreal forests gaps threatens natural

regeneration of these native species by exerting harmful allelopathic effects on the survival of new emergents.

Conversely, survival of transplanted nursery-derived seedlings was not negatively affected by Canada thistle over their first year in the field, suggesting that these larger seedlings are capable of co-existing alongside dense Canada thistle monocultures. There was no detectable allelopathic impact on these larger balsam fir after the first complete year transplanted within Canada thistle monocultures. However, long-term monitoring is required to determine whether larger fir seedlings/saplings remain resistant to allelopathic effects over time. These larger seedlings also avoided the large loss to early seedling herbivores experienced by newly emerged fir seedlings. The greatest impact on the growth and survival of transplanted seedlings was not Canada thistle, but moose herbivory.

The need for active restoration

Active restoration will be required to achieve the formation of mature forest within non-regenerating forest gaps in Gros Morne National Park. Even under conditions of significantly reduced moose densities, these altered forest gaps will likely encounter other barriers to natural succession and regeneration. Some of these barriers include the poor condition of seedbeds for conifer establishment, the high level of invasion of these gaps by Canada thistle (which inhibits the early establishment of balsam fir and white spruce) and other non-native species, and the low levels of balsam fir emergence from seed, particularly within anthropogenic gaps. A successful restoration program to

encourage balsam fir regeneration and canopy formation in Gros Morne National Park will require at least two main steps: 1) reducing moose densities, which are the primary cause of the regeneration delay and alien plant invasion, and 2) encouraging growth of native trees within forest gaps through a planting program. Reduction of moose impact must be the first step for gap restoration to be successful in the long-term. Where high moose populations compromise restoration of ecological integrity and conflict with clearly defined goals for ecosystem management, as they clearly do in Gros Morne National Park, there is support in national parks policy for intervention (Corbett 1995, Parks Canada Agency 2000).

This study found that sowing balsam fir seeds is not an efficient approach to encouraging gap regeneration in Gros Morne National Park due to high rates of loss to early seedling herbivores, negative impacts of Canada thistle on balsam fir emergence and early survival, and the high variability of success among gaps. Rather, planting greenhouse-established seedlings to rapidly reestablish balsam fir within gaps and to accelerate canopy formation is a better way to promote natural successional processes within gaps. As there were no negative effects of growing these larger seedlings within Canada thistle monocultures for one complete year, and there were even slight advantages to growing amongst thistle, the planting of balsam fir seedlings could be a viable and promising management step to encourage canopy formation both within invaded and uninvaded areas of gaps and could also act to slowly phase out growth of shade-intolerant Canada thistle over time.

Such an ecosystem approach to management is preferable to targeting aggressive control efforts solely towards Canada thistle in this protected forest system since the problem of invasion is rooted in large-scale changes to ecosystem processes and disturbance regimes (Chapin et al. 2000, Myers and Bazely 2003). As well, conventional invasive plant control efforts in natural areas often seriously threaten native species, alter ecosystem structure, and stimulate further invasions (Hobbs and Humphries 1995, Zimdahl 2004, Smith et al. 2006). Future research on methods of controlling widespread and uncontained invasive plant populations within natural lands must shift away from the familiar focus on destructive chemical and mechanical eradication techniques, and move towards developing less-intrusive control methods suitable for sensitive areas which encourage native community development and phase out growth of exotic ruderals. Mack et al. (2000) also note that to be successful, non-native plant management must account for the factors that promote ecosystem invasion, including change in disturbance regime, change in resource status, and increases in propagule pressure. In Gros Morne National Park, a decrease in hyperabundant moose densities would be the first step in addressing all of these underlying drivers of alien plant invasion. Indeed, a shift in emphasis from strict invasives management towards broader ecosystem restoration goals is required (Zavaleta et al. 2001).

Other specific management suggestions for Gros Morne National Park

- Due to high variability in success among individual gaps, any planting program would greatly benefit from an initial evaluation of the suitability of local

environmental conditions. As well, small-scale planting trials to evaluate success of a proposed planting program within any particular targeted gap may be advantageous to identify potential pitfalls before initiating large-scale restoration and making large financial investments.

- Planting balsam fir seedlings (at least 25 cm in height) is preferable over the sowing of seeds. Where planted among Canada thistle, success of seedlings must be monitored to determine if there will be an impact of allelopathy over the long-term. Canada thistle vigour should also be monitored to determine if it can be effectively shaded out over time.

- It is <u>not</u> recommended that mycorrhizal inoculations be routinely performed in any re-introductions of balsam fir, white spruce, or white birch seeds or seedlings within gaps. In greenhouse trials in field-derived soil, inoculations were shown to have no effect on growth or survival of these species and to significantly decrease emergence of seeds; further field trials may be desirable to confirm its lack of merit.

- Independent efforts to mechanically control Canada thistle through hand cutting or digging up individual plants does not improve success of balsam fir emergence, growth, or survival growing amongst thistle and thus is not recommended during planting of fir.

- Potential pathways of movement for Canada thistle seeds into remote sites must be minimized. Monitoring should be performed along moose trails and hiking paths throughout Gros Morne National Park to detect and remove newly established Canada thistle populations before they spread further along the corridor of disturbance and invade new gaps. Such 'search and destroy' approaches to the removal of alien plants have often been successful in natural areas such as parks and organized volunteers can usually readily be found (Mosquin 1997).

- Early detection of the presence of a small, isolated population of an invasive non-native plant can make the difference between being able to initiate successful offensive strategies (e.g. eradication) as opposed to having to retreat to a defensive strategy, which may be ineffective and costly (Rejmánek and Pitcairn 2002). New and/or small infestations are most likely to be successfully eradicated and thus should be given immediate management priority when first detected (Nuzzo 1997, Rejmánek and Pitcairn 2002).

- In any management activities within Canada thistle-invaded gaps, including invasive plant control or the planting of native trees, it is important to consider the allelopathic potential of Canada thistle biomass and its associated soil. For instance, if Canada thistle control is initiated where a small-scale or new infestation has occurred, all biomass should be removed from the site and not left to decay *in situ*.

- In addition to Canada thistle, other common invasive alien plants present within forest gaps included coltsfoot (*Tussilago farfara*), hawkweeds (*Hieracium spp.*), buttercups (*Ranunculus repens, R. acris*), and common dandelions (*Taraxacum officinale*); populations of these species in particular should be closely monitored throughout the Park's natural areas and efforts initiated to remove any small colonizations within gaps. Further research is required to determine if these non-native plants also threaten forest regeneration.

- Zavaleta et al. (2001) stress that although in most settings, removing or reducing introduced herbivores is the most important first step in ecosystem restoration, the response of exotic plant populations to decreased browsing pressure can sometimes be unpredictable. Since Canada thistle is not browsed by moose, it is expected that release of competing plant species from browse suppression within gaps will only aid in combating this non-native invader. Additionally, a reduction in moose densities is predicted to minimize future problems of regeneration failure and alien plant invasion in newly formed gaps. Still, close monitoring after herbivore reductions, as well as pre-reduction assessments, can help reduce the potential for unexpected negative consequences of invasive alien plants (Zavaleta et al. 2001).

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APPENDIX I:

Characteristics of Boreal Forest Gaps Surveyed in Gros Morne National Park, NL

Table A.I. – Characteristics of 24 boreal forest gaps in Gros Morne National Park, NL, surveyed during the summer of 2006.

Disturbance Regime	Gap Abbreviation	Full Gap Name	Thistle in Gap?	UTM (NAD 83) (East/North)	Distance From Road (m)	Elevation (m)	Period of Disturbance
Natural Gaps (Insect Kill)	BBB	Baker's Brook site B	×	433199/5498375	1566	96	1987
	BHC	Berry Hill Campground	×	433199/5497433	30	180	1987
	LOA	Lomond site A	×	444033/5479048	754	95	1987
	RBC	Rocky Barachois site C	×	447847/5481115	964	149	1987
	SCV[a]	Sally's Cove	×	435201/5512503		5	1987
	WWA	Wigwam Pond site A	×	454685/5470808	599	41	1987
	BBA	Baker's Brook site A	✓	432989/5497845	605	76	1987
	LOB	Lomond site B	✓	443585/5479048	1241	34	1987
	SPA	St. Paul's site A	✓	449086/5521623	6580	75	1977
	SPB	St. Paul's site B	✓	449277/5521735	6732	77	1977
	WWB	Wigwam Pond site B	✓	454507/5474005	854	35	1987
Anthropogenic Gaps (Harvested)	302	302*	×	444431/5475655	388	163	1990-94
	401	401*	×	442078/5476543	376	303	1980-88
	402	402*	×	441160/5476743	218	295	1989-2004
	GLN	Glenburnie	×	435482/5475506	400	46	1983-89
	MBC[a]	Mill Brook site C	×	443383/5483680		70	1987
	MBD[a]	Mill Brook site D	×	443594/5483871		113	1983
	SEB	Southeast Brook	×	451180/5478609	350	104	1994-2004
	SEI[a]	Southeast Brook inner site	×	450612/5478066		106	1994-2004
	MBA	Mill Brook site A	✓	443513/5483778	613	77	1987
	MBB	Mill Brook site B	✓	443623/5483859	735	99	1983
	RBA	Rocky Barachois site A	✓	447116/5481694	100	69	2000
	RBB[a]	Rocky Barachois site B	✓	447275/5481575	100	66	1996
	TKB	Tucker's Brook	✓	443665/5483379	653	56	1997

*Gap numbers correspond to those used in 2005 *"Parks Canada Forest Regeneration Surveys of Domestic Timber Harvest Blocks"*

[a]Only transect survey was performed; seedbed surveys not performed

APPENDIX II:

Gap-Specific Soil Moisture and Temperature Conditions

Table A.II. – Mean (±SE) percent soil moisture (2006, 2007) and soil temperature at 10 cm depth (2007) in three treatment locations within five anthropogenic forest gaps and five natural gaps in Gros Morne National Park, NL. All gaps were invaded by Canada thistle and undergoing balsam fir seed addition experiments. Treatment abbreviations: UG = uninvaded gap; UE = uninvaded forest edge; T = Canada thistle monoculture.

Disturbance Regime	Gap	Treatment	% Soil Moisture 2006[b]		% Soil Moisture 2007		Soil Temperature 2007 (°C)	
			Mean	SE	Mean	SE	Mean	SE
Anthropogenic	**MBA**	UG	3.62	0.24	2.12	0.02	12.97	0.13
		UE	2.25	0.47	1.07	0.10	9.95	0.21
		T	3.56	0.19	2.39	0.01	12.80	0.20
		Total	***3.09***	***0.30***	***1.86***	***0.20***	***11.81***	***0.46***
	MBB[a]	UG	4.02	0.09	2.55	0.03	11.85	0.18
		UE	4.38	0.76	2.59	0.06	11.20	0.06
		T	3.96	0.17	3.25	0.03	13.97	0.09
		Total	***4.12***	***0.22***	***2.80***	***0.12***	***12.29***	***0.38***
	RBA	UG	2.30	0.00	*	*	*	*
		UE	0.50	0.07	*	*	*	*
		T	0.85	0.05	*	*	*	*
		Total	***1.00***	***0.34***	*	*	*	*
	RBB	UG	2.79	0.00	*	*	*	*
		UE	3.44	0.04	*	*	*	*
		T	3.58	0.00	*	*	*	*
		Total	***3.31***	***0.18***	*	*	*	*
	TKB[a]	UG	3.83	0.17	3.83	0.05	13.53	0.34
		UE	4.22	0.13	4.72	0.03	10.78	0.38
		T	2.75	0.60	4.15	0.02	14.38	0.15
		Total	***3.70***	***0.26***	***4.23***	***0.13***	***12.89***	***0.49***

Table A2 continued ...

Disturbance Regime	Gap	Treatment	% Soil Moisture 2006[b]		% Soil Moisture 2007		Soil Temperature 2007 (°C)	
			Mean	SE	Mean	SE	Mean	SE
Natural	**BBA**[a]	UG	1.94	1.26	0.54	0.02	12.37	0.15
		UE	1.97	0.75	3.64	0.03	9.17	0.19
		T	3.14	0.00	1.51	0.03	16.85	0.15
		Total	***2.16***	***0.51***	***1.89***	***0.46***	***12.29***	***1.13***
	LOB	UG	2.65	0.00	0.62	0.00	11.83	0.13
		UE	0.89	0.21	0.78	0.01	11.23	0.32
		T	0.69	0.14	0.95	0.00	13.03	0.17
		Total	***1.05***	***0.28***	***0.78***	***0.05***	***12.01***	***0.26***
	SPA	UG	1.31	1.06	0.65	0.00	11.97	0.13
		UE	0.48	0.00	0.46	0.02	11.88	0.20
		T	1.90	0.00	0.56	0.07	12.38	0.79
		Total	***1.25***	***0.52***	***0.56***	***0.03***	***12.08***	***0.28***
	SPB[a]	UG	0.29	0.03	0.31	0.01	14.35	0.36
		UE	0.35	0.00	0.46	0.02	11.88	0.20
		T	0.74	0.27	0.88	0.03	14.68	0.55
		Total	***0.48***	***0.13***	***0.55***	***0.10***	***14.51***	***0.31***
	WWB	UG	0.78	0.18	0.43	0.04	11.80	0.00
		UE	1.44	0.37	2.16	0.01	10.00	0.20
		T	1.51	0.00	1.59	0.02	12.35	0.05
		Total	***1.17***	***0.21***	***1.39***	***0.25***	***11.38***	***0.45***

* Data missing (black bears occupied sites during sampling periods)

[a] Gaps also undergoing balsam fir seedling addition in 2007

[b] Data shown for 2006 % soil moisture data are averaged across three summer sampling periods

APPENDIX III:

Results of Allelopathy Experiment 2 in Potting Soil That Are Not Contained in Chapter 4 (Section 4.3)

Emergence:

White birch in potting soil

Emergence of white birch planted in potting soil did not differ significantly among treatments ($\chi^2 = 3.61$, df = 3, p = 0.3071). Mycorrhizae additions significantly decreased birch emergence in potting soil by 35% of the control (No mycorr: 67.8% ± 4.3%; Mycorr: 44.3% ± 4.8%; $\chi^2 = 12.91$, df = 1, p = 0.0003).

Time to Emergence:

White birch in potting soil

In potting soil, the time to birch emergence differed significantly among treatments ($\chi^2 = 8.45$, df = 3, p = 0.0376) however only the *–C.a.* versus *–C.a.*$_{AC}$ contrast was significant (p = 0.0047), with AC addition to *–C.a.* soil increasing the time to emergence by an average of 2.9 days.

Mycorrhizal fungi inoculation did not affect the time to white birch emergence in potting soil ($\chi^2 = 1.74$, df = 1, p = 0.1874).

Balsam fir in potting soil

The number of days to emergence differed considerably among treatments for balsam fir in potting soil (treatment $\chi^2 = 9.83$, df = 3, p = 0.0201), with seedlings

emerging 1.8 days earlier on average in +*C.a.* soil than in –*C.a.* soil ($p = 0.0337$). Addition of activated charcoal to +*C.a.* soil significantly increased the emergence time by 2.4 days ($p = 0.0044$) but did not significantly change the time to emergence in –*C.a.* soil ($p = 0.1987$).

White spruce in potting soil

The time to emergence for white spruce did not significantly differ among treatments for seeds planted in potting soil (treatment $\chi^2 = 3.50$, $df = 3$, $p = 0.3203$).

Survival:

Balsam fir in potting soil

Balsam fir survival in potting soil differed significantly among treatments ($\chi^2 = 9.23$, $df = 3$, $p = 0.0264$), yet survival in +*C.a.* potting soil did not differ from –*C.a.* soil ($p = 0.4346$). Addition of activated charcoal decreased survival by 21.3% in non-thistle soil (–*C.a.* vs. –$C.a._{AC}$, $p = 0.0117$), but did not lower survival in +*C.a.* soil (+*C.a.* vs. +$C.a._{AC}$, $p = 0.7846$).

Biomass:

White spruce in potting soil

In potting soil, the effect of treatment on spruce aboveground biomass was dependent upon whether mycorrhizae addition had occurred (treatment*mycorr: $F_{3,72} = 3.87$, $p = 0.0127$; treatment: $F_{3,72} = 2.10$, $p = 0.1076$; mycorr: $F_{1,72} = 0.93$, $p = 0.3388$).

Further splitting of the model (by the mycorrhizae factor) revealed that spruce aboveground biomass in potting soil differed significantly among treatments only when mycorrhizae addition had occurred ($F_{3,36} = 5.80$, $p = 0.0024$), and contrasts indicated this difference was due primarily to a decrease in seedling biomass after activated charcoal addition to *–C.a.* soil (*–C.a.* vs. $–C.a._{AC}$; $p = 0.0056$; Figure A.III. *a-b*). Belowground white spruce biomass in potting soil was not affected by mycorrhizal addition (treatment*mycorr: $F_{3,72} = 2.01$, $p = 0.1201$; mycorr: $F_{1,72} = 2.02$, $p = 0.1600$) but did vary among treatments ($F_{3,72} = 4.72$, $p = 0.0046$). Again, this difference was a result of a decrease in belowground biomass resulting from activated charcoal addition to *–C.a.* soil (*–C.a.* vs. $–C.a._{AC}$; $p = 0.0010$).

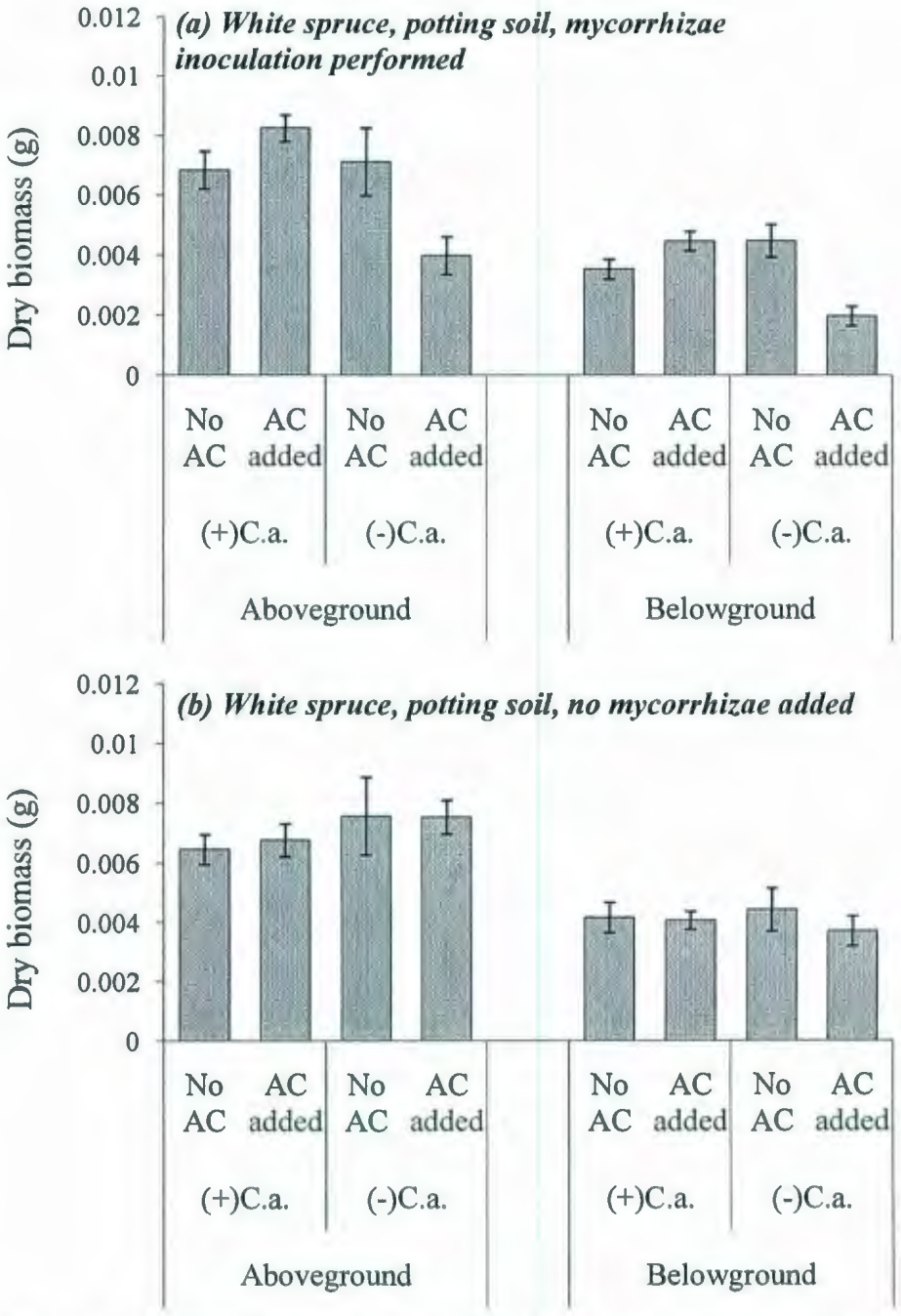

Figure A.III. – Effects of previous Canada thistle growth in potting soil and activated charcoal addition to potting soil on the aboveground and belowground dry biomass of a) white spruce seedlings receiving mycorrhizal inoculations, and b) white spruce seedlings not receiving mycorrhizal fungi. Seedlings were harvested for determination of biomass 10 weeks after planting of seeds. Each bar represents n=10 seedlings. AC = activated charcoal; (+)*C.a.* = soil which supported previous growth of *Cirsium arvense*; (-)*C.a.* = soil which did not support growth of *C. arvense*. Bars indicate ± standard error.

APPENDIX IV:

GPS Locations of Seedling Addition Experimental Plots

Table A.IV. – GPS locations of balsam fir seedling addition experimental plots which have been left intact within Gros Morne National Park, NL. Seedling addition was performed using 15 month old balsam fir seedlings obtained from Wooddale Provincial Tree Nursery, Newfoundland (Dept. of Natural Resources, Government of NL), which originated from balsam fir seeds collected from western Newfoundland. Seedlings were planted within four gaps in the summer of 2007 and each gap contained three replicate plots for four treatments: T = Canada thistle monoculture, T_{-A} = Canada thistle monoculture with shoots removed, UG = uninvaded gap, UE = uninvaded forest edge. Each plot (n=48 total) was planted with nine fir seedlings, spaced in a 3 × 3 block at 1 m distance on all sides. Seedlings averaged 24.7 cm in height at planting.

Gap	Treatment	Plot #	UTM (NAD 83)	
			Easting	Northing
TKB	T	1	443691	5483434
(Tucker's Brook)	T	2	443685	5483437
	T	3	443682	5483450
	T_{-A}	1	443676	5483443
	T_{-A}	2	443672	5483417
	T_{-A}	3	443684	5483453
	UG	1	443705	5483457
	UG	2	443700	5483462
	UG	3	443675	5483364
	UE	1	443685	5483370
	UE	2	443649	5483367
	UE	3	443661	5483320
MBB	T	1	443626	5483866
(Mill Brook site B)	T	2	443639	5483898
	T	3	443608	5483836
	T_{-A}	1	443616	5483842
	T_{-A}	2	443632	5483851
	T_{-A}	3	443626	5483864
	UG	1	443606	5483858
	UG	2	443631	5483878
	UG	3	443632	5483886
	UE	1	443624	5483888
	UE	2	443616	5483861
	UE	3	443587	5483836

SPB	T	1	449306	5521789
(St. Paul's site B)	T	2	449306	5521797
	T	3	449301	5521812
	T_{-A}	1	449293	5521802
	T_{-A}	2	449304	5521803
	T_{-A}	3	449304	5521792
	UG	1	449290	5521797
	UG	2	449288	5521784
	UG	3	449269	5521738
	UE	1	449330	5521773
	UE	2	449244	5521660
	UE	3	449056	5521485
BBA	T	1	433006	5497740
(Baker's Brook site A)	T	2	433003	5497750
	T	3	433006	5497755
	T_{-A}	1	433008	5497737
	T_{-A}	2	433009	5497749
	T_{-A}	3	433009	5497756
	UG	1	433004	5497843
	UG	2	432983	5497884
	UG	3	433042	5497811
	UE	1	433046	5497784
	UE	2	432967	5497755
	UE	3	433059	5497948